

THE DIVERSITY OF THE INSECT FAUNA OF FOUR SPECIES
OF *NOCTUAE MOLINII* IN GAINESVILLE AND
ITS RELATIONSHIP TO THE PLANT ARCHITECTURE.

By

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for my husband, Ray

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THE BIOLOGY OF THE INSECT FAUNA OF FOUR SPECIES
OF SOLENOX (COMPOSITAE) IN GAINESVILLE AND
ITS RELATIONSHIP TO THE PLANT ARCHITECTURE.

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The insect fauna of four species of goldenrods, *Solidago canadensis*,
S. rigida, *S. serotina* and *S. nemoralis* were surveyed during four
years in Gainesville, Florida. The 126 phytophagous and 126 beneficial
(including spiders and pollinators) species are listed and classified
according to frequency, galls, host range, part of the plant attacked,
life stages collected, and associated goldenrod species. Only 15 of the
phytophagous species were restricted to goldenrods and *Ager*. Thirteen
of these are discussed and the eight galls are schematically illustrated.

Leaf water and nitrogen contents of the leaves of the four *Solidago*
species significantly affected development and fecundity of two specialist
herbivores: *Galleria latens* (Diptera: Tephritidae) and *Agrogonus phloxalis*
(Tortricidae). *S. rigida* leaves had higher water and nitrogen content

and was the preferred host for both insects. J. canadensis had significantly lower leaf nitrogen content but performance of both insects on this host was equivalent to performance on J. glauca and J. incanaberris because of the low leaf water content of these two plant species.

The insect population was surveyed and the number of leaves, leaf area, plant height and flower stalks also were determined for each species of goldenrod during four periods of the growing season in 1983 and 1984. Total leaf area best explained the variation in insect diversity among the three localities studied. Plant frequency, local abundance and environmental factors also had a detectable effect on this variance. Chemical defenses and nutritional quality of the host plant may be responsible for unexplained variability.

The seasonal build up of the insect fauna closely fits Lawton's (1983) hypothetical model for the interaction between plant architecture and chemical defenses as changes in the insect community during the growing season of a perennial herb.

Seven insects are noted as possible biological control agents: Lygus erich. (Lygus attacking roots), Phytomyza distincta and Spizella lutea (leaf chewers), Agropyron sp. f and Dendrochrysa salicivora (leaf miners), Acanthosia carbonacea (leaf gill miner), Ichneumon confusus (weed feeder) and Schizocampa ruficornis (flower gill miner).

Brinsmead act as a reservoir for many beneficial insects, but for only a few pest insects.

INTRODUCTION

Plants of the genus Elymus are widespread throughout the con-
tinent. About 18 species of this perennial herb occur in Florida
(Howell, 1980). Four species are more likely to be found in the old
fields, fence rows, or roadsides in the Gainesville area. They are
Elymus canadensis L. var. canadensis (Pursh) (referred to here as E. canadensis
(Werner et al., 1984) E. flexuosus Miller, E. giganteus Nelson and E.
trisetus (L.) K. & G. E. canadensis var. glauca and E. giganteus range
naturally throughout the eastern region, from Florida to Canada, and have
been introduced to Europe (Capin, 1871). E. canadensis also occurs in
Japan (Ito et al., 1971). E. flexuosus and E. trisetus are confined
to the southeastern region of U.S. (Hornquist, 1980). These four species
can be easily distinguished from each other by differences in size, form,
and structure of the leaves and inflorescence, and in flower phenology.
All four species begin to grow in late March and are down to rhizomes in
the beginning of December. They build up their structure each year, as
leaves, stems, flowers and seeds are added to the plant through the
growing season. None of these species is a pest of cultivated fields in
the United States. However, E. canadensis var. glauca is a host for some
diseases that also attack economically important crops (Parker and
Anderson, 1978; Werner et al., 1984). It also increases allelopathic
substances that inhibit germination and growth of surrounding vegetation
(Lickens et al., 1970). This species and E. giganteus are noxious weeds
of reforestation areas and forest nurseries in Europe. A biological
control program of goldenrods was proposed by Capin (1911) and Zeltner

(1986). A survey of natural enemies to identify potential biological control agents is now taking place in North America (Hein et al., 1984).

On the other hand, these plant species have some beneficial properties that could be explored in their native land, where they are not considered weeds. *S. jacobina* var. *spinos* is an alternative source of food for arthropod predators and parasitoids of crop pests (Giliardi, 1978). It also produces chemical substances that have insecticidal characteristics (Ramos et al., 1977). Weederless plants are an important source of pollen and nectar in late fall (Kassal, 1982).

The general objective of this study is to present basic information on the insect community structure of goldensrod. Such information is relevant if goldensrod is to be cultivated, either as beneficial plants that should be maintained or even enhanced, or as undesirable plants that should be controlled. A biological control program could proceed faster and be less expensive if better predictions could be made as to which of the phytophagous insects would be good candidates for biological control agents. The chance of finding successful agents increases with the knowledge of the predation of polyphage among phytophagous insects related to the target weed (Landon and Schneider, 1981).

To access information on the interaction between the insect community and goldensrod plants, and their implications, the following points will be considered:

1. The abundance of the different taxa of insects on goldensrod and their relationship to the structural characteristics and phenology of the host species.
2. The specificity of phytophagous insects and their distribution by pollen.

2. The correlation between the total number of insect species and the arthropod complexity of the host plant.

3. The life history strategies of two phytophagous insects most frequently found in *Silene* spp., considering food and oviposition preferences among the four hosts studied.

LITERATURE REVIEW

Ecological Role of Solanaceae

The genus Solidago belongs to the tribe Astereae of the family Compositae. Plants of this genus are found in a variety of environments, from dry to sterile soil, sand, and soils enriched to fertile land of wet forests; from open, abandoned old fields to shady woods (Capek, 1971; Hesse, 1988). It is represented by more than 100 species distributed in the Americas, Eurasia, Africa (Parnicki, 1988) and Japan (Takeuchi, 1980). Most of the species are endemic to North America, a few to South America and Eurasia and one to the Azores (Parnicki, 1988).

Solanaceae are perennial herbs, characteristic of secondary succession. They reproduce vegetatively by rhizomes, and usually by producing great numbers of light seeds (Marner et al., 1988).

The large blossoms of goldenrods make them very attractive as ornamental plants. They are adapted to a variety of conditions (Hesse, 1988) and bloom from summer to late fall, when most other plants have ceased flowering. Goldenrod blossoms are also valued by landscape, since they are one of the few sources of pollen and honey in late fall (Hoffman-Sandig and Lonsdale, 1979; Toris, 1979; Polakow and Sander, 1977; Benintesa and Marquisse, 1988). Some pollinator insects such as bumblebees (Schuch, 1978; Toris, 1979) and honeybees (Olson, 1979; Rabari and Kaulian, 1978) prefer the easily accessible flowers of goldenrods. Psithyrus fasciatus (L.), a social wasp, and the lesser Spangulium rufum (Parnicki) selectively visited blossoms of Solidago canadensis among the various fall flowering plants in their goldenrod

fields in southwest Ohio (Blackwell and Powell, 1971). The most pollinators of goldenrods are honeybees (*Apis mellifera* Linn.), bumblebees (*Bombus* sp.), solitary bees (*Oxytrichus pennsylvanicus* (Gefner)) and syrphid flies (Warner et al., 1980). Some mosquitoes also feed on nectar of *Solidago* spp., among other plant species (Ragland, 1977; Schmalzer and Schaller, 1979).

Goldenrods have other useful properties. Leaves of the most goldenrod (*S. agrostifolia*) make an insect-flavored tea and, if boiled in water, make a green dye that can be used for fabrics (Blackwell, 1981). *S. canadensis* L. and *S. rigida* L. showed potential as sprays and rubber protecting trees (Huchman et al., 1979). *S. rigida* L. and *S. agrostifolia* can be used for oil production (Lawrence, 1979; Aristakis and Brachman, 1972). Perhaps the most investigated property of *Solidago* spp. is their chemical constitution (Chlorson, 1977; Ragauer, 1973, and Hara, 1977). Compounds such as diterpenes, glycosides, flavonoids and saponins were extracted from goldenrod plants (Miller et al., 1979, 1981; Brachman et al., 1979; Hara et al., 1982). A survey in the USSR showed that *S. rigida* was among 25 species of plants used to treat cellulitis, suggesting that its chemical properties should be scientifically investigated (Blackwell, 1970). Some of the chemical substances in goldenrods may also have insecticidal properties. Male codlingmoths, *Carpocapsa pomonella* L., are stimulated by extracts of the leaves of *S. altissima* (Widlin and Pasvick, 1978). Insects exposed to these extracts showed characteristic nervous behavior. A synthetic extract of residues of *S. altissima* incorporated into the diet completely inhibited hatching of eggs of *Scaphisoma californicum* (Hewitt et al., 1977).

Some of the substances produced by *Solidago* spp. inhibit germination and growth of the surrounding vegetation (Kitchner et al., 1978). This allelopathic effect of goldenrod plants may have important economic implications. For example, growth of black locust was reduced 80% by adding dried foliage of *S. canadensis* var. *serotina* (= *S. altissima*) to the soil (Larson and Schwarz, 1981). A water extract of *S. gigantea* Ait. inhibited height growth, secondary root formation and dry weight increments of *Pinus resinosa* Ait. seedlings (Nebel and Kucharski, 1981). Germination, nutrient uptake and growth of young sugar maple (*Acer saccharum* Michx.) was inhibited by water soluble components produced by *Solidago* spp. (Pinner et al., 1981). The production of these allelopathic substances make goldenrods strong competitors. This trait, associated with rapid vegetative reproduction, allows them to form dense stands, crowding out other vegetation. In certain regions of Europe, where goldenrods have been introduced, they damage seedlings as well as young and old trees in reforestation areas. Goldenrods are replacing the native vegetation, consequently reducing the indigenous phytophagous and entomophagous insect populations because they seldom feed on it. Goldenrods are now considered aggressive pests of forest nurseries in Europe (Zedler, 1976). In Japan, goldenrods have become one of the most dominant weeds on railway right of ways, roadsides and other outcrop situations, near urban areas (Ito et al., 1976). *S. canadensis* (Opalin?), *S. canadensis* var. *serotina* (= *S. altissima*) and *S. gigantea* have wide distributions and were imported some 180 years ago into Europe by gardeners (Capek, 1971). Since then these three species may become tenacious weeds they are now rarely recommended as ornamentals (Zedler, 1976; Capek, 1971; Pinner, 1977). *S. canadensis* var. *serotina* is now one

of the most economically rationalized plants in Japan (Takahaya, 1980).

Studies on chemical control of goldenrod show that some herbicides are effective against this plant. *S. canadensis* is susceptible to 2,4-D and picloram in Quebec. It is also affected by paraquat, glifosate and alaron, but susceptibility to these treatments declines with age (Fiorini and Rees, 1979). Glifosate + saccharose + 2,4-D proved to be effective to control *S. canadensis* var. *gledits* (= *S. albidum*) in Germany (Anonymous, 1979). Glifosate alone had no effect on this species in Indiana blueberry fields in Canada (James, 1979). In Japan, *S. canadensis* var. *gledits* (= *S. albidum*) was completely controlled by post-emergence application of azadir, flurochlorac, thiazofluorac and isuron (Ito et al., 1979), and azoxystrobin + alaron (Mishiguchi and Ito, 1979). Chemical control of *Solidago* spp. was reported by Barlett and Palmer (1972), Williams and Russell (1973), Barling et al. (1976), Lowrance and Peters (1976), Peters and Lowrance (1976), Jensen (1977), Gentry and Gentry (1980) and Peters (1982). In forest nurseries and reforestation areas of Europe, where goldenrods are aggressive and troublesome weeds, they are controlled by costly mechanical measures or by applying herbicides in high concentration (Jullier, 1976). This is expensive and carries the risk of environmental contamination.

Goldenrods have several characteristics of good candidates for biological control. It is a structurally complex plant, with several points of attack to phytophagous insects. Although the aerial parts die down each winter, the rhizomes are available throughout the year, presenting an ecological continuity. This would be important in establishing and building up a population of natural enemies. Goldenrods, imported to Europe and Japan from North America, are free from their

native entomofauna. Damage caused by the indigenous phytophagous insects is only minor and sporadic (Capek, 1871; Edliff, 1878). In North America however, many phytophagous insects are found associated with the widely distributed goldenrods. Many of them, restricted to the genus Heliothis, cause severe damage in certain regions of Eastern Canada (Ford and Hammer, 1974) and the United States (Oertwein and Aeschmann, 1979; Penland and Root, 1980). Ford et al. (1978) recorded 46 moth species from S. canadensis in southeastern Ontario. Over 80% of this moth fauna belong to a group of seven species which form a characteristic sequence of initial occurrence from early to late season. In central New York, Penland (1978) reports 23 species of moths associated with old field goldenrods (Heliothis spp.). Only six genera accounted for 87% of all individuals which can be divided into 3 distinctive guilds, some feed on goldenrod flowers and others feed on the immature foliage. The tarnished plant bug, Largus lineolaris (F. & S.), was the most common species. The leaf beetle fauna associated with Heliothis spp. in central New York is composed of nine specialists (species that feed only on goldenrod and related), four generalists, and seven facultative. The specialists, Trichodes elongatus Lef. and S. horvathi Blake, account for 64% of all the beetles collected (Penland and Root, 1980). Goldenrods host many species of insects which stimulate gall production on stem, leaf, root, or inflorescence (Harris, 1984). These gall insects may play an important role in the evolution of the plant life history patterns. Stem galls of Gaucha pallidivittata (Fitch) (Tephritidae) and Spinywaya gallarumellus(Gill) (Hymenoptera: Halictidae) cause a decrease of 44% and 20%, respectively, in root propagule production (Stewart and Shreeves, 1979). The presence of these two galls and the gall of Amelanchier

gall-forming saw (Cecidomyiidae) increased stem production, decreased current inflorescence production, and lowered seed reproductive allocation of L. canadensis (Barbott and Richardson, 1978). Occurrence of either gall can have an appreciable impact on the fitness of the plants.

The possibilities for the biological control of gall-formers in Europe were fully discussed by Capen (1971) and Jelliffe (1976). Capen (1971) surveyed, during one year, populations of L. canadensis, L. canadensis var. pubens and L. angustata in Ontario. He recorded insects injurious to roots, stems, leaves, flowers and seeds. He recommended further studies on the following insects as potential biological control agents: two tephritid species that bore roots and stems, Ecotoma dorsalis Wier, and L. dorsidorsatus Girdling Clem., three species of stem-gall makers, Stemoxys galligena Fitch, Stemoxys canadensis Clem., and Stemoxys galligena Fitch, and the leaf feeder Trichomyia canadensis (Og.). The author reported this beetle as being the most important phytophagous species on goldenrods in Canada. Further studies (Raid and Harris, 1978) showed, however, that L. borealis and not L. canadensis is the major defoliator of L. canadensis in southeastern Ontario. Jelliffe (1976) complemented Capen's studies by discussing the conflict of interests with the beekeepers and giving guidelines for further research. Jelliffe and Harris (personal communication) grouped the insects reported from Gallium spp. in a list sorted by order, superfamily and gall. In Japan, the cecidoid moth Agropyrum glaberrima (Fr. Gr.) is reported as the major defoliator of L. canadensis var. pubens (= L. angustata). This species is being studied as a possible biological control agent (Jennings, 1980).

In the United States, goldenrods are also, in many cases, considered harmful plants. It is generally believed that goldenrod causes hay fever. However, unlike other plants such as ragweed, grasses and sedges, goldenrod pollen is not widespread but is transported from plant to plant by a variety of pollinators such as bees, beetles, butterflies and birds (Owen et al., 1981; Blackwell and Powell, 1981; Foster, 1982). In reality, the sticky florets of goldenrods are being blamed for the hay fever caused by the inappreciable flowers of other plants.

Although the hay fever problem is a myth, the number of disease-producing organisms hosted by goldenrod is a fact. Some of these organisms attack plants of economic importance. For example, E. cinerariae hosts Cynophya cinerariae B. G. an agent (primary effector) which attacks crucifers and composites, Phytomyza cineraria (Ozier) Dup. (pink rot) which also occurs on cotton and sugar beets, and Colletes willughbi which is a fungus attacking Flax carolina Rtt., E. helveticus Lam. and E. cylindrica L. (Webb's and Anderson, 1974; Warner et al., 1982). Callitige sp. also hosts Colletesporium sphaeri that attacks Christmas-trees in plantations and nurseries (Dunn, 1952) and Phak helveticus (Anderson and Anderson, 1974).

Goldenrod may be an alternate host for pest insects that would migrate to the surrounding goldenrod fields when crop plants are no longer available. It could, on the other hand, host beneficial insects such as predators and parasitoids that would fly to crop fields and keep pest populations low. Otterl (1981) cites several examples in which the incidence of important pests is reduced by maintaining the natural weed vegetation at the border or within crop fields. The weeds offer an alternate source of food, shelter, overwintering sites, breeding and

writing areas for important predators, and pollen and nectar for parasitoids of crop pests. L. canadensis var. montana (? = L. ruficollis) is cited as one example of a weed that provides an alternate food resource (the aphids, Uroleiscus sp.) for predaceous arthropods (Dacnusa spp., Chorebus sp., Andrena spp., Spilostoma, spiders and others) (Altieri, 1970). The tube-celled elliptical galls caused on the stems of L. gigantea by the herbivore moth Lythraea nassoides (Clem.) are an important host resource for parasitic insects in northwestern Pennsylvania. Of 12 primary parasitoids that emerged in the spring of 1975 and 1976 from these galls, seven were known to parasitize a variety of insect pests during their summer generations (Flukider, 1978). Bergeson and O'Neil (1980) reported that galls on Lythraea sp., mainly on L. canadensis and L. grandifolia (L.), provide 80% overwintering, 1.7% Spilostoma and 0.6% Andrena. A natural population of the grasshopper Hesperotettix viridis pratensis Say, in North Dakota declined and disappeared due to a high rate of infestation with the weevils Baris elegans Say. Other grasshopper species were uninfested or had low rates of infestation. The high percentage of infestation in H. viridis pratensis was related to a low wet habitat, where the grasshoppers fed primarily on Lythraea alnifoliaris Nutt. (Chengakoff and Burford, 1973).

Surveys of insects related to a given plant species or to a plant trade frequently have as objectives the identification of potential pest species to the plant itself or to other economically important plants. Surveys are also made to search for biological control agents. A survey of predaceous insects would serve both purposes and would detect the presence of important predators and parasitoids of crop pests. Such

information would be of major importance for the understanding of the ecological role of this plant in agroecosystems.

Section 4: *Phytosapra* & Function of Plant Archiophages

Solidworts host a great diversity of phytosapras and archiophages insects. Fane (1944) reported 260 species on *L. grandis* var. *glaucoglossum* Rydb. and *L. canadensis* var. *holzeri* (L. Hitchcock), in a single year. Several characteristics of the host plant influence the number of insect species associated with it: It was suggested earlier (Northwood, 1965) that the diversity of the assemblage of a given taxon increases with the range of the plant and is linearly correlated with the geological age of the plant taxon. In other words, the number of insect species associated with a given taxon would increase slowly and continuously at least first, over long periods of geological time. There is evidence, however, that an equilibrium of the insect community occurs in ecological time. Present conditions are important in determining insect diversity, and it has been shown that the equilibrium reached depends largely on the geographical range of the plant (Strong, 1976a,b,c; Simberloff, 1984). When geographically close and similar areas are considered, the larger the range of the plant, the larger the number of phytosapras species associated with it. This principle is based on MacArthur and Wilson's equilibrium theory of island biogeography which predicts that "the number of species of a particular taxonomic group on an island will reach equilibrium, and that the equilibrium number of species is a function both of the area of the island and its distance from the species source" (Simberloff, 1984).

Jensen (1971) suggested that "host plants are islands in a sea of competition for phytosapras insects". Following this point of view, the

theory of island biogeography has been extended to include any situation where isolated, discrete patches of habitat are surrounded by dissimilar areas. Sayer (1944) tested this hypothesis by examining the relationship between 134 species of leaf-mining insects and the range of their 28 host species of oaks. He found that species number increases curvilinearly with increasing area. Many other studies have confirmed that host geographical range is the most important determinant of the number of species associated with a host plant (Southwood, 1960, 1961; Southwood et al., 1982; Lawton and Schröder, 1977, 1978; Strong and Lawton, 1978; Cramer et al., 1988; Cornell and Haselhorn, 1979; Lawton and Price, 1979; Strong et al., 1977; Claridge and Wilson, 1987; Cornell, 1984). More widespread plants are more likely to be found and colonized by insect species adapted to the various climatic situations covered by the plant's geographical range. Indeed, Foster and Lawton (1980) showed that the number of habitats occupied by each species of umbellifer in Scandinavia (England) had a marked effect upon associated species richness, with plants that grow in more habitats supporting more species of insects.

Area per se, however, is not the only mechanism responsible for species-richness. For instance, Lawton and Schröder (1977) compared observed species-area curves for perennial herbs, woody shrubs, weeds and other annuals and monocots. They found a statistically significant difference in intercept among the regression lines of these five kinds of plants. For a given size of geographical range, each group of plants has a characteristic number of insect species associated with it. The number of insect species associated with woody shrubs is equal that of perennial herbs, which is larger than weeds and other annuals, which in turn is larger than monocots (woody shrubs larger than perennial herbs but not

statistically significant). They next tested the effect of taxonomic isolation on diversity of a plant's entomofauna, based on the idea that species with several relatives in the same geographical area will exchange herbivores more easily than unshared plant species (the authors used the word exchange in refer to the "equilibrium of a herbivore guild on an evolutionary time scale"). Only composites provided evidence to support this notion, and it could not account for the differences in intercept among the regression lines. After eliminating the "apparent" explanation of leafy [LSH] leafy shrubs are more apparent and thus more likely to have higher colonization and lower extinction rates than weeds and composites) because composites had even less insects associated with them than weeds and other annuals, the authors suggested that the richness of the insect fauna was a function of plant architecture... Individual species of plants have different growth forms. They vary in number of suitable habitats provided for phytophagous organisms and in physical size of the individuals. They also vary in average local plant density and in chemical characteristics. This individual variation between plant species influences the number of insect species associated with them. When plants with a similar size of geographical range are compared, the richness of associated insect fauna follows the sequence *Imperianisidicaria* (Lewin and Schröder, 1977) *Sorbus*, 1977, *Strong* and *Lewis*, 1981, i.e., it decreases with the decrease in architectural complexity of the plants.

The term "architecture" is defined by Lewin (1982) as "a variety of plant attributes such as size and growth form, seasonal development, persistence and variety of above ground parts". Plants with a more complex architecture have more niches available for phytophagous insects.

as well as for predators and parasites, supporting a bigger qualitative species pool. Lawton (1983) discusses the two hypothesis that might explain the effects of the components of architecture: the size per se hypothesis and the resource diversity hypothesis. The size per se hypothesis states that larger plants are more apparent and thus more likely to be found and collected by insects, in ecological and evolutionary time, than are small plants. If the number of insect species on a plant is a balance between colonization and extinction, then larger plants lose more species associated with them because they have a reduced extinction rate. As Lawton (1983) reports, very few experiments are available demonstrating the effect of size on species richness because size and resource diversity are often positively correlated and it is difficult to discern the contributions of each one to the faunal diversity. The resource diversity hypothesis states that plants that have more feeding, resting, breeding, overwintering and hiding places available support more insect species than plants with fewer resources. Plants with greater diversity in their basic feeding sites are likely to be more insect species-rich, at least in part because most insects are specialized in their host choices. Lack of a particular structure, for instance the absence of flowers and fruits in trees, exclude specialized herbivores (Lawton, 1983). Other resources such as shelter, oviposition and overwintering sites and a place to hide from natural enemies are also important requirements for phytophagous insects. These resources are more available on more architecturally complex plants, such as trees and shrubs than on simple ones, such as herbs. Trees and shrubs have available a variation in stem/culmlets, foliage chemistry and toughness, permitting a variation of herbivores either vertically, on arboreal plants,

or horizontally, across plants of different ages. Other factors to be considered as availability of resources are the seasonal changes in the general palatability of the foliage and stem (chemistry, toughness, etc.) that might cause a turnover of seasonal specialist insects. Plant species with large seasonal changes in their palatability should be attacked by a greater variety of insects than other plant species which show less change.

Due to great variability in the ways plants differ as resources available to herbivores, it seems that resource diversity is the major contributor to the patterns of insect diversity. Yet, as noted before, resource diversity varies in parallel with size, and one can hardly be excluded from the other.

There is evidence, besides that already cited, of the influence of plant architecture on the diversity of phytophagous insects that is consistent with one, or another, or both hypotheses discussed above. Burdick et al. (1972) sampled plants and thrips in three old fields in southeast Michigan. They found that insect diversity was highly correlated with the foliage height diversity over all three fields. The species richness of coleopterid beetles on *Pinus* trees and shrubs is explained by the frequency of the host plant, number of relatives, plant height and leaf size (Deane and Masella, 1981). Deciduous plants growing vertically supported a greater number of the corymbid beetles, *Chrysomelids* (Fab.), than plants growing horizontally (Sack, 1980). Among the two oak species in the New Jersey tidal salt marshes, *Quercus prinus* (Mill.) forms a dense and persistent thicket, while *Quercus alternifolia* (L.) produces only a loose lattice of thinner stems rapidly decaying. Whiffin has determined that the thicket of the *Q. prinus*

population is responsible for the larger assemblage of sap-feeding insects on this species than on *L. alamosa* (Benson, 1977). In another study, Tallamy and Spence (1989) compared the structurally simple grass, *Spartina alterniflora* with a structurally complex one, *Distichlis spicata* (L.). They found that *D. spicata* exhibited a richer and more diverse community of sap-feeders than *L. alamosa*. Species richness of red-leaf hoppers feeding in Central America is correlated with host species range, size, and diversity (Strong, 1977). Woody bushes and shrubs in Europe support more species of herbivore insects than perennial herbs of the same species. Individual species of British trees are attacked, on average, by more species of aphidophagous than are shrubs and both are attacked more than herbs (Price, 1971).

The effects of variation changes on resource availability are noted by Cameron (1980), Thompson and Price (1982) and Thompson (1980). In each case, additional species enter the system to utilize the resources that are added to the plant as the season progresses. Effects of plant architecture are not just apparent in gross comparisons between major growth forms and taxa. It can also be detected among closely related groups of species. Plant size and growth form of plants of the family *Umbelliferae* within the British Isles have a significant effect on the number of species of aphidoid leaf-mining larvae (Carter and Price, 1976). Moran (1980) analyzed the insect community of 28 species of *Spartina*, 14 large and 14 small. Among 127 species he found a highly significant correlation between the total number of phytophagous insects and a measure of the overall architecture of their host plants. The criteria used to calculate the architectural rating were height of plants, stem number and area of clade, development of woody stems and

spatial complexity. Price and Wilson (1978) showed that larger species of aphid on alfalfa support more species of specialized herbivores than small ones.

The positive relationship between species richness and host complexity is not universal, however. For example, the number of cynipid gall-wasps on large species of North American oaks are not notably higher than on small species (Cornell and Rickman, 1993). This may be a reflection of the difficulty in detecting architectural effects within a closely related group of plants (Larson, 1993).

The architectural complexity of the host plant may affect the life history strategies of insects. For instance, Saloff (1983) suggested that the almost complete absence of filigreed moths in some groups of temperate Hemiptera and Heteroptera in arboreal habitats (in contrast with their low incidence in grasses and forbs) is related to the architectural complexity of trees. Leaves and branches of a tree are usually more widely spaced than those of grasses and forbs. Insects as a class have greater freedom of movement in all three dimensions and the relationship of wings and the ability to fly may be more advantageous than brachyptery. However, Blum (1988) dismissed Saloff's hypothesis claiming that architectural complexity of trees are not favorably staged for individuals or species, although it may have done so in some Hemiptera.

In temperate regions, there is a seasonal progression of the fauna on a plant. The number of phytophagous insect species on a patch of broomrape generally, reaching a peak in late July and early August, with very few being found on the plant throughout the whole season (Larson, 1993). In a first analysis of these data, the author suggested that the variation in number of species of phytophagous insects

was due to a declining quality of leaves as food during the growing season, because during most of the summer the quality of proteins in the plants is considerably below that usually regarded as optimal for many insects. At the same time, there is an increase in the levels of tannins, lignin and cellulose. Lawton's findings were very similar to those of Jeap (1974) on leaves of oak trees, and both authors agreed on the plant chemistry explanation for the seasonal variation in the phytophagous fauna of leaves and oak. However, Lawton (1970) expressed the idea that plant architecture instead of plant chemistry might better explain the variation in the number of insect species throughout the year.

The Nutritional Quality of Host Plants

While host range and plant architecture influence the number of insect species on a plant, plant defense strategies (including nutritional, chemical, physical and behavioral mechanisms) affect the kind of insects which inhabit the plants. Less than a third of the terrestrial arthropods have achieved the ability to feed on land plants (Southwood, 1972), apparently because of the difficulties that phytophagous organisms face in overcoming plant defense mechanisms. Plants are known to produce allelochemicals such as alkaloids, flavonoids, terpenoid oils, glycosides, resins and lignins (Bryksson, 1972) which affect growth, behavior and population dynamics of phytophagous insects (Rousse, 1974). In the course of their coevolution with the host, insects responded to these plants' defenses by evolving detoxifying mechanisms (Deluge, 1982). After overcoming this difficulty, phytophagous insects still have to face nutritional barriers. Increased research on insect nutritional ecology has revealed that host plants are often nutritionally sub-optimal, and that insects have evolved

physiological and behavioral adaptations to compensate for this difficulty (McNeill and Southwood, 1938). The nutritional value of a host plant has great influence on the components of an insect's life history strategies such as body size, generation time, fecundity and dispersal behavior (Slansky, 1982). Basic nutritional requirements of phytophagous insects are energy, nitrogen and water (Barbier and Slansky, 1981). The role of nitrogen in the herbivores' diet was fully discussed by McNeill and Southwood (1938) and Malaise (1940). Slansky and Feeny (1982) tested the effect of varying nitrogen content on larval growth of the cabbage butterfly, *Pieris rapae* L.). They compared the larval growth on several different plant species and on plants of a single species in which the nitrogen content has been increased to various levels by chemical fertilization. The results showed that nitrogen is the limiting supply in all normal food plants and that the larvae adjust their feeding rates to maintain nitrogen accumulation rate and hence the rate at which they can grow on a given host. Many other studies have demonstrated effects of nitrogen content of the diet on growth and reproduction of lepidopterous larvae (Rodriguez, 1940; Feeny, 1979; Southwood, 1972; Grossman, 1975, 1976; Scriber, 1979a, b; Barbier and Feeny, 1981) as well as in other insects (see Gates, 1966; Stone, 1970; Schultz, 1972; Scriber and Schoonhoven, 1981) including beetles (Taylor and Barber, 1940; Schram, 1973; Fox and Knevel, 1977). Peave (1973) studied the effect of plant species on fecundity, longevity and weight of the mustard beetle *Phaedon cochleariae* Fabricius. Best performance of the beetle was achieved on turnip. Fecundity was reduced on mustard, Chinese cabbage and brassica sprouts. At a given age, total nitrogen content of turnip was higher than that of the other plants.

Plants show seasonal variation in their chemical constitution, higher concentrations of nitrogen (3-7% of dry weight) occur in young or storage tissues (such as seeds). Nitrogen content declines gradually throughout the growing season until senescence, when it drops sharply (3.5-4.5%) (Maltison, 1980). Nitrogen content of leaves of *Brassica hirta* callifera (B. 4 B.) was negatively correlated with leaf age and decreased during the growing season (Johnson et al., 1984). Feeding by larvae of fall webworm, *Hyphantria cunea* (Drury), on early spring nitrogen-rich foliage results in greater development and fecundity compared with insects feeding on late spring foliage (Kates, 1986). In the contrary, larvae of *Spilophora corymbosa* (L.) grow faster when fed with low instead of high nitrogen content leaves (Schneider, 1971).

Increasing nitrogen availability through fertilization increases plant susceptibility to insect attack (Scriber, 1980). Larvae of the fall armyworm *Spodoptera frugiperda* (L. 16th) and the corn earworm *Bombix mori* (L.) feed more voraciously, develop faster, and have lower mortality when fed with corn plants fertilized with high rates of nitrogen (Whitson, 1971).

Besides the fact that low nitrogen may cause substantial changes in plant nitrogen (Maltison, 1980), and thus affect the development of phytophagous organisms, leaf water content may directly influence the metabolic costs, efficiencies and growth rates of Lepidoptera (Pruett and Beck, 1976; Scriber, 1977). Like total nitrogen, leaf water also declines with age (Scriber and Blaisdell, 1981). Leaf water content on young trees in Poland declines from 72% in June to 57% in August-September, along with a decline in nitrogen from over 3% to less than 1%. This change in leaf water and nitrogen caused a reduction in the

assimilation of food efficiency for Lepidoptera from 80 to 99-100 (Matsuya et al., 1978).

From the information above it is expected that phytophagous insects would discriminate among different host plants, selecting the species with higher water and nitrogen contents. Other factors, however, influence food choices of a particular insect. Hardness of the leaves (Shawson, 1965), host finding and recognition, and natural selection (Southwood, 1972) are factors that also have to be considered in the selection of a particular host.

STUDIES AND METHODS

General Community of Galtonville

The total flora of Galtonville was surveyed for four consecutive years in Mississippi, Florida. The collections started in June of 1981, stopped during the winter and resumed again in April of 1982. In the first year, surveys were made on galtonville populations in the Gainesville area that were large enough to be spotted from a car. In 1982, 18 of these populations were selected of which two were surveyed each week.

The following galtonville species were found: Solidago canadensis var. scabra (Pursh), L. fruticosa Miller, L. gigantea Allen and L. latifolia L. & G. L. canadensis var. scabra is far more common than the other species (11 of the 18 populations) and is found on hanks, roadsides and clearings in sunny areas. L. fruticosa is the second most common species. It occurs in old abandoned fields forming large stands sometimes mixed with blackberries. Only one small stand of L. gigantea was found on a poorly drained roadside. L. latifolia is sparse and usually mixed with many other weeds. The population used for this study occurs on a small bank, in a very disturbed area. All four species started to grow in March but they vary in flowering time. L. latifolia and L. gigantea flower late in August. L. fruticosa blooms in middle September and L. canadensis var. scabra in late September. From 1981 to 1983 the galtonville stands were completely dead by the beginning of December.

In 1985, three populations of L. canadensis and two of L. fruticosa were selected, and together with the populations of L. gigantea and L.

~~insects~~ were set as study sites. A standardized survey was made on these seven populations during four periods of the growing season: early May, middle July, before flowering (+ 10 days) August or early September and just after flowering (late September or early October). Collections in 1984 were made only on E. canadensis var. rubra and E. ~~canadensis~~ (see below).

The insects and plants were identified by specialists from the University of Florida, Department of Agriculture and Consumer Services and the USM Systematic Entomology Laboratory, c/o U.S. National Museum. Adult voucher specimens were placed in the Florida State Collection of Arthropods, excluding three species of Coccinellidae that were retained by Dr. R. E. Snodgrass. The immature voucher specimens were placed in the immature insect collection of the Department of Entomology and Nematology, maintained by Dr. G. E. Snodgrass.

A phytophagous species was considered common if it was present in at least 50% of the collections. Occasional species were those collected in 1% to 50% of the samples and rare if present in less than 10% of the samples. Insects collected only once during the four years were excluded, as well as those collected often but known to be incidental and associated with other plants such as Tribolium haemorrhoidale Weber. Those species that fed only on Malvaceae and Solanaceae were considered monophagous. Those whose host range included plants belonging to families other than Compositae were considered polyphagous.

Among the beneficial insects, common species were collected in at least 10% of the samples. Those present were then once in a given plant species sample were reclassified and those collected only once were rare.

Host Suitability of *Scylliops* species For
Schizothrips luteipes (LaSalle)

Larval and Adult Performance

This experiment was done in two consecutive years. In the first year the larvae used were the offspring of males and females collected in the field which were fed a different species of palmerid each test day. In the second year adults were fed only with the plant species on which they were collected.

Each treatment had 30 replications in the first year and 40 in the second year. These consisted of one newly hatched larva put in a small, transparent 1-liter plastic cup containing a mixture of agar with fungicide and bactericide in the bottom. Four treatments were run, one for each of the palmerid species. The larvae were fed twice a week with young fresh leaves of one of the plant species. In the second year's experiment they were given the same kind of food as their parents. (These females were not collected on *S. [pennsylvanicus]* until late in the season, larvae for this treatment were obtained from eggs of females collected on *S. thurberianus*. The eggs were maintained in an environmental chamber at about 27°C and 60% humidity. When the prepupae started to spin cocoons, daily checks were made and date of pupation and adult emergence were recorded.

Newly emerged adults were weighed on a Mettler balance and were then fed with the same plant species on which they had been reared. Beetles were sexed three or four days after emergence, when the females's abdomen became fully developed and the males could be easily distinguished from them. After being sexed, one male and one female, both from the same treatment, were put together in a small plastic cup with agar and fed

with their original plant species. The age at first egg laying, the number of eggs laid per day, the number of days the female laid eggs and the life span of males and females were recorded from this second set of experiments.

Feeding and Oviposition Preference

Female choice of host species for oviposition was tested in a cylindrical cage, 28 cm high and 28 cm diameter. Small vials containing water were stuck to the bottom of the cage, equally spaced from each other. Fresh, equal sized stems of the four species of Salicags were placed one in each vial. Ten males and one female of L. latrans were released in the center of the cage which was topped with water and then completely covered with a plastic bag to maintain plant turgor. Plant species position inside the cages and the position of cages inside the environmental chamber were rotated. The temperature inside the chamber was maintained at 22°C, 40% humidity and 14 hours light, 10 hours dark photoperiod. The cages were checked after 24 hours. The plant species on which eggs were laid, the number of eggs, and the plant species on which male and female were feeding were recorded. This experiment had four treatments one for each of the four potential species on which the beetles were reared. The number of replicates was variable due to the reduced availability of adults reared as L. glaucus and L. insularis.

Experiment 5:

Host Suitability of Salicags species for Leptogaster divinus divinus

Larval and Adult Performance

The experiment to measure larval performance consisted of one newly hatched larva put in a small, transparent plastic cup containing a

medium of agar and fungicide and bactericide (described earlier). The larvae were the offspring of males and females reared on *S. rigidosus*. Four treatments with 20 replications were run. In each treatment, fresh, young leaves were provided every two days to the larvae. The cups were maintained in an environmental chamber at 21°C, 60% humidity and 12 hours light/20 hours dark photoperiod. When the last instar larval leaves appeared, daily checks were made. Newly molted pupae were weighed within 24 hrs of pupation in a Mettler balance.

The adults were reared on one male and one female, both from the same treatment were put in a gallon size tin drum carton covered with transparent plastic. Food was provided by a cotton ball soaked with 20% sugar solution. A water-filled bottle was placed in the center of the carton. One fresh stem of the plant species on which the male and the female were reared was placed inside the bottle to provide orientation clues. Adult performance was measured by recording the number of eggs laid per female and the life span of males and females.

Life Cycle of *Delia* *integrus* and *Spartanoxenus* *distinctus*

Information on the life cycle of *D. integrus* and *S. distinctus* was obtained from field observations and laboratory experiments. Mature larvae were collected and reared to adults in the laboratory. Young larvae of one of the palisaded species were provided two or three times a week. Females were allowed to mate and lay eggs following the procedures described previously. When the eggs hatched the larvae were isolated in 1 ounce clear plastic cups with agar medium. Two replications for each plant species were run. The duration of each larval instar was determined by checking the cups daily looking for larval skins and head

capsules. The duration of the pupal stage and adult life span were also recorded.

Water and Nitrogen Contents

The nutritional value of the food plant was determined based on the water and nitrogen content of the leaves of each host plant. Samples of leaves taken from plants collected twice a week to feed the weevils were weighed on a Mettler balance and dried for three days at 70°C. The samples consisted of about 10 g of young leaves excised from each of the plant species. The procedure was repeated for five weeks, giving a total of 10 samples. The water content of the food plant was determined by the difference in weight between fresh and dried leaves. Total nitrogen of the same leaves was determined by a Microkjeldahl technique (Nelson and Sommers, 1970) and was expressed as % of dry weight.

Plant Architecture and Insect Behavior

The four plant species were measured in 1983 and 1984 to obtain an estimate of their architectural complexity. The three populations of *J. canadensis* var. *scabra* measured were located on the border of woods. Two of them (B. P. East and B. P. West) were in a small ditch on a roadside and the other one (Black P.) in an abandoned field along a roadside. The plant stands were of approximately the same size, the largest was about 25 m². *J. floridana* was measured in two locations. In one of them (O.S. 441) the palmetto stand formed a strip adjacent to a sandy field dominated by grasses and ferns. The soil was wet and sandy. This population was moved before the study was completed. At the other location (SR 15 Ave.) *J. floridana* invaded a large, abandoned field of about 80 m² on a roadside. The population of *J. ligustica* (Buckwheat Rd) was described previously. It occupied an area of about 50 m² on the

border of a large weedy field (mostly Euphorbia, Aster and some species of Leguminosae). L. inaequalis had the smallest population of all (Anchor Rd) and has also already been described. Small patches of plants were scattered among other weeds. The whole area covered about 18 m².

The density of plants in the different populations of each of the four plant species is shown in Table 1.

In 1981 measurements were made at four growing stages, as explained before: May, July, September and October. Architectural differences were considerable only between L. canadensis var. guttata and L. inaequalis. The measurements were then repeated in these two species in 1984. Since the plants did not present significant changes between

Table 1. Average densities of plants (no. of stems/m²) in the 7 populations of Salpiglossis.

Plant Species	Location	No. of Stems/m ²
<u>L. canadensis</u>	B. P. East	75
	B. P. West	100
	Rocky P.	30
<u>L. fulva</u>	U.S. 890	12
	W 14 Ave.	260
<u>L. glabra</u>	Washburn Rd.	94
<u>L. inaequalis</u>	Anchor Rd.	121

September and October, only one measurement was made between these two dates in 1984. Thus the plants were measured in May, July and late September.

Each sample consisted of 40 similar sized plants collected by cutting the stem at the soil line. The following measurements were taken from each plant: height, number of leaves, leaf area, and number and size of flowering stalks, if present. All leaves potentially available as a source of food for phytophagous insects were counted, except for the modified leaves of the inflorescence. The leaf area of each plant was determined by averaging the areas of ten leaves, measured with a leaf area meter.

RESULTS AND DISCUSSION

The Insect Community of *Salicapsa*

The Phytophagous Fauna

Eight orders, 42 families and 124 species of phytophagous insects were found associated with *Salicapsa* spp. in Salinasville. Of the 124 species, 42 (34%) feed on this plant. The weevils *Agrostus quadricornis* (Say), the chalcidid *Chlorocelis glauca* Fowler and the delphacid *Prionoxystus marginatus* Van Duzee were new Alachua County records, and the grasshopper *Cromalopteryx pallidipes* Foy and Ball, was a new state record.

Of the 122 phytophagous insect species associated with *Salicapsa* or *Grisebilla*, 15 feed only on *Salicapsa* or on *Salicapsa* and *Aster*, seven also feed on other plants of the family Compositae, and 58 are polyphagous, i.e., feed on a variety of plants from different families. Fig. 1 shows a schematic drawing of *S. filifolia* and the number of phytophagous insects in each order feeding on the different parts of the plant. The great majority of the polyphagous insects are saprophages from the order Homoptera (34) and Isoptera (44), collected from leaves, stems and flowers. The chalcidids were the most represented group with 14 species, six of which were common. The psocids were represented by seven species, divided by six and by one. Two chalcids, *Agrothia lineatella* (Felt, in Germ.), *Agrothia pallidipes* (Stueben), and three psocids, *Agrostus quadricornis* (Say), *Agrostus viridis* (L.) and *Agrostus rufus* (F.) are of economic importance. *Agrostus lineatella*, the terrestrial plant bug, occurs on a great variety of wild and cultivated

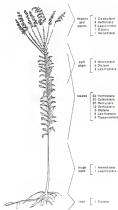


Figure 2: Schematic drawing of a tall, slender plant and the number of phytosociological orders and species in each order feeding on the different parts of the plant.

Table 2. continued

Gerridae: 10 spp.

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La, P1	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La, P1	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	P1	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La, P1	St	St	P1

Dipteridae

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St	P1

Hemiptera

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	P1	St	St, St	P1
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Gerridae: 10 spp.

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St	P1
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Dipteridae

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St	P1
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Hemiptera: 10 spp.

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	P1	St	St, St, St	P1
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Dipteridae

Dipteridae

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A, P1	P1	St	St	P1

Dipteridae

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A, P1	La	St	St, St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St, St, St	P1

Dipteridae

<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A	La	St	St, St	P1
<i>Stenonema</i> <i>Stenonema</i> (Stenonema)	C	A, P1	La, St	St	St, St, St	P1

Table 3, continued

Rubiaceae

<i>Psychotria hirsuta</i> (Sw.) Pav. 1918, 1920, 1921, 1922	1	L, A	20	20	20, 21, 22, 23	P ₂
<i>Psychotria hirsuta</i> (Sw.) Pav. 1918, 1920, 1921, 1922	1	L, A	20	20	20, 21	P ₂
<i>Psychotria hirsuta</i> (Sw.) Pav. 1918, 1920, 1921, 1922	1	A	20	20	20, 21, 22, 23	P ₂
<i>Psychotria hirsuta</i> (Sw.) Pav. 1918, 1920, 1921, 1922	1	A	20	20	20, 21	P ₂

Pythiaceae

<i>Pythium</i> sp.	1	L, A	20	20	20, 21	P ₂
<i>Pythium</i> sp.	1	A	20	20	20, 21	P ₂

Rubiaceae

Rubiaceae

<i>Rubiaceae</i> sp.	1	L, P, A	20	20	20, 21	P ₂
<i>Rubiaceae</i> sp.	1	L, P, A	20	20	20, 21	P ₂
<i>Rubiaceae</i> sp.	1	L, P, A	20	20	20	P ₂

Rubiaceae

<i>Rubiaceae</i> sp.	1	L, P, A	20	20	20, 21	P ₂
<i>Rubiaceae</i> sp.	1	L, A	20	20	20, 21	P ₂
<i>Rubiaceae</i> sp.	1	L, P, A	20, 21	20	20, 21, 22	P ₂

Rubiaceae

<i>Rubiaceae</i> sp.	1	L, P, A	20	20	20, 21, 22	P ₂
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Rubiaceae

<i>Rubiaceae</i> sp.	1	P, A	20	20	20	P ₂
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Rubiaceae

<i>Rubiaceae</i> sp.	1	L, P, A	20	20	20	P ₂
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Rubiaceae

<i>Rubiaceae</i> sp.	1	L, A	20	20	20, 21, 22, 23	P ₂
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Table 2, continued

Terrestrial						
<i>Phalaena</i> <i>Phalaena</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂
<i>Phalaena</i> <i>Phalaena</i> <i>Chen</i>	8	L ₂	P ₁	Ch	Sc	P ₁
<i>Phalaena</i> <i>Phalaena</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	L ₁	Sc, P ₁ , P ₂ , P ₃	P ₁
Aquatic						
Amphipoda						
Amphipoda						
<i>Amphipoda</i> <i>Amphipoda</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	Ch	Sc, P ₁ , P ₂	P ₂
<i>Amphipoda</i> <i>Amphipoda</i> <i>Chen</i>	8	L	L ₂	Ch	Sc, P ₁ , P ₂ , P ₃	P ₂
<i>Amphipoda</i> <i>Amphipoda</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	Ch	Sc, P ₁ , P ₂	P ₂
<i>Amphipoda</i> <i>Amphipoda</i> <i>Chen</i>	8	L	L ₂	Ch	P ₁	P ₁
Crustacea						
Crustacea						
<i>Crustacea</i> <i>Crustacea</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	Ch	Sc	P ₂
Hydromedusa						
Hydromedusa						
<i>Hydromedusa</i> <i>Hydromedusa</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	Ch	Sc, P ₁ , P ₂ , P ₃	P ₂
<i>Hydromedusa</i> <i>Hydromedusa</i> <i>Chen</i>	8	L ₂	L ₂	Ch	Sc, P ₁	P ₂
<i>Hydromedusa</i> <i>Hydromedusa</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂
Polychaeta						
Polychaeta						
<i>Polychaeta</i> <i>Polychaeta</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	Ch	Sc	P ₂
<i>Polychaeta</i> <i>Polychaeta</i> <i>Chen</i>	8	L	L ₂	Ch	Sc, P ₁	P ₂
<i>Polychaeta</i> <i>Polychaeta</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂
Scaphopoda						
Scaphopoda						
<i>Scaphopoda</i> <i>Scaphopoda</i> <i>Chen</i>	8	L ₂ , L ₃	L ₂	Ch	Sc	P ₂
<i>Scaphopoda</i> <i>Scaphopoda</i> <i>Chen</i>	8	L	L ₂	Ch	Sc, P ₁	P ₂
<i>Scaphopoda</i> <i>Scaphopoda</i> <i>Chen</i>	8	L	L ₂	Ch	Sc, P ₁	P ₂
Stomatopoda						
Stomatopoda						
<i>Stomatopoda</i> <i>Stomatopoda</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂
<i>Stomatopoda</i> <i>Stomatopoda</i> <i>Chen</i>	8	L	L ₂	Ch	Sc, P ₁	P ₂
<i>Stomatopoda</i> <i>Stomatopoda</i> <i>Chen</i>	8	L	L ₂	Ch	Sc, P ₁	P ₂
Tunicata						
Tunicata						
<i>Tunicata</i> <i>Tunicata</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂
<i>Tunicata</i> <i>Tunicata</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂
<i>Tunicata</i> <i>Tunicata</i> <i>Chen</i>	8	L	L ₂	Ch	Sc	P ₂

Table 2. (continued)

<u>Terminological dimension</u>	<u>E</u>	<u>L</u>	<u>Le</u>	<u>Se</u>	<u>St</u>	<u>Pg</u>
<hr/>						
^a <u>E</u> = larvae; <u>L</u> = additional; <u>Le</u> = none						
^b <u>E</u> = eggs; <u>L</u> = larvae; <u>P</u> = pupae; <u>St</u> = adult						
^c <u>Le</u> = larvae; <u>St</u> = stage; <u>Pt</u> = flowers; <u>St</u> = seeds						
^d <u>St</u> = closed egg; <u>Se</u> = yellowish; <u>St</u> = silver; <u>Se</u> = brown; <u>St</u> = healthy; <u>St</u> = healthy						
^e <u>St</u> = <u>Salix caprea</u> ; <u>St</u> = <u>S. caprea</u> ; <u>St</u> = <u>S. caprea</u> ; <u>St</u> = <u>S. caprea</u>						
^f <u>St</u> = <u>Salix caprea</u> ; <u>St</u> = <u>S. caprea</u> ; <u>St</u> = <u>S. caprea</u> ; <u>St</u> = <u>S. caprea</u>						
^g <u>St</u> = <u>Salix caprea</u> ; <u>St</u> = <u>S. caprea</u> ; <u>St</u> = <u>S. caprea</u> ; <u>St</u> = <u>S. caprea</u>						

plants. It feeds on the tender growing or fruiting parts causing serious damage to crops (Hurrell et al., 1954; Sefcault and Flish, 1961). Adults of this insect were collected from May to October on three of the four species of goldenrods: G. tinctoria, G. gigantea and G. canadensis. Epiclerus pallidus attacks a variety of wild plants. When abundant, this species can be a pest of ornamentals (P. W. Reed, personal communication). It feeds and breeds on all four species of goldenrod studied and is very common throughout the year. Among the cistophilids, the southern green stink bug, Boisdu valida, is the most significant, since it is an important pest of tobacco and other crops. It feeds mainly on Leguminosae (Tord and Roush, 1960), but it was found feeding and breeding from May to July on three of the four species of goldenrods.

Most of the plant chewers were also polyphagous. Of 12 species of chrysomelids, only Chrysomella integriceps (Gyll.) is restricted to Solidago and Sparganium angustifolium Fab., which was rare and collected only on G. angustifolium. Feeds on plants of the family Compositae. Chrysomelids alticola (Gyll.) Barber, the spotted cucumber beetle, was the only economic species among the chrysomelids. Adults were collected a few times on the leaves of G. canadensis and G. tinctoria.

Polyphagy in lepidoptera was restricted to the three geometrids and two of the tortricids. All species of Orthoptera collected are polyphagous.

Among the insects feeding on Solidago spp. and other Compositae, the leafhopper Corythosba nana (Giller) and the psyllid corn Siphonophorus pallidus (Fitch) were collected on the four goldenrod species. C. nana was very abundant and eggs, nymphs and adults were found at the plant throughout the growing season. S. pallidus was

also common. The eggs of this moth are laid on the growing tip of young goldenrod plants. The new larva comes downward into the soft, new stem, before reaching what is apparently the third instar it leaves the upper part of the plant stem through a lateral hole and moves down to the mature, older stem. It makes another hole as it goes down the ground and buries downward to the roots. The larvae pupates inside the stem, close to the entering hole, through which the newly emerged adult leaves the plant. The upper part of the plant, where the young larvae bore, withers and dies. Infested plants can be recognized by the dried tips. Young larvae are collected on the plant in May and mature ones can be found as late as October. This is a good indication that more than one generation is involved.

The other two carpenter beetles commonly found were the goldenrod Trichostema flavicollis (Germers) and T. punctum White. These species cause considerable damage to the goldenrods. The former is a leaf miner and the latter bores inside the growing tip, interrupting the terminal growth of the plant.

Rest of the species restricted to the genus Salix were aphidophagous - they make galls on leaves, flowers, stem and roots, and flower and leaf miners. The others are a seed feeder, Stenus medianus (Gory), a sap feeder, Chrysomelids marci (Fabric), a leaf miner, Phryganidia dissecta (Hollingshead), and a leaf chewer, Agrotis leptus (Guil.). The latter two insects will be the subject of following chapters. The others will be discussed here. The general distribution of seven specific insects is shown in Figure 2.

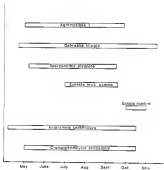


Figure 2. Seasonal distribution of the feeding stages of the most common insects specific to lettuce crop in Gainesville, Florida. Note: The end of the bars indicated that life cycle is not known.

The black or white leaf blister galls of *Asteromyia carbonifera* (Deten Sachse) (Fig. 3.1) were frequently present on the four species of goldenrod during the four years of collection. The number of galls per leaf is variable, from one to several, sometimes covering the whole leaf blade. The relationship between *A. carbonifera* and the fungus that infects its gall was discussed by Hirst (1964). The galls are the result of both fungus and insect activity. It appears that *A. carbonifera* associates with leaves of goldenrod already infected by the fungus *Helicostictia asteris* (Kotw.) . Two or three larvae of the wasp develop between layers of this fungus that form a chamber on either side of the larval chamber. Wells (1962) showed that the formation of the virus constitutes an important mechanism of protection against attack of the parasite *Torymus rapae* (Holar). In Salinasville, the gall ridges larvae were frequently parasitized by *Tetraneura* sp. 1, *T. horrid* (Grossi), and *T. hesperus* Burks, of the family Halictidae.

Another leaf blister gall found occasionally on the leaves of the goldenrod species studied is made by a wasp identified as *Asteromyia* sp. nr. *carbonifera* (Deten Sachse). The galls are greenish, circular, often surrounded by a purplish necrotic area on the leaf (Fig. 3.2). They were heavily parasitized by *Aspilota* sp. (Grossi), of the family Spilidae.

Aspilota sp. nr. *carbonifera* (Deten Sachse) makes a gall in developing buds. It establishes itself between the surface of the larvae while they are still in the bud and as a result of the tissue action the adjacent tissues form an oval cell between the two surfaces. The leaves continue their normal development but grow attached to each other at the point where the gall developed (Fig. 3.3). A common parasite of these species was *Helicostictia harrisi* (Walker), of the family Halictidae.



Figure 3. Spindlered galls in Azerbaijan. 1, Althaea leaf galls of *Aphidius arbutus*; 2, leaf gall of *Aphidius arbutus*; 3, stem galls of *Aphidius arbutus*; 4, flower galls of *Aphidius arbutus*; 5, root galls of *Aphidius arbutus*; 6, stem galls of *Aphidius arbutus*; 7, leaf galls of *Aphidius arbutus*; 8, leaf galls of *Aphidius arbutus*.

Sheffer damage is caused by the edge Scirpomyia sp. on the four species of goldenrod, although only the injury on the developing, opened leaves of the graydog had was observed. No adult was reared from the reddish larvae, thus the species could not be determined.

Scirpomyia pallidipennis is another gall midge that attacks the buds, transforming them into globular masses of deformed leaflets (Fig. 3.8). In the center of the mass, a cylindrical chamber with tapered apex shelters the yellowish larva. This gall was seen only occasionally on all goldenrod species but S. canadensis. It was also parasitized by S. hirsuta.

The larva of Scirpomyia sp. develops inside individual globular galls with a tapered apex. These galls develop together forming an aggregation on the stem (Fig. 3.8). Scirpomyia sp. was collected occasionally, only on S. fistulosa. The parasite was Jaegeria sp. or Apeltesia (Rohrer), probably a new species, was reared several times from this gall.

The only flower gall observed in this study was made by the edge Scirpomyia ruscigalla (Gross & LaSalle). It produced a rounded gall with tapered apex, frequently reddish, on the stems of S. canadensis and S. fistulosa (Fig. 3.9). The larvae are orange-red, and they leave the gall when disturbed.

The apical masses of Scirpomyia pallidipennis galls were occasionally seen on the stems of S. fistulosa and S. gigantea in Greenville (Fig. 3.8). A complete description of the biology of this insect is given by Kelly (1988). It is widely distributed and has also been reported from S. canadensis, S. nemoralis and S. parviflora. Yellow green galls are found from July on through the winter in Greenville. In

North Carolina this insect hibernates in the egg stage (Lefly, 1932), but in Florida it apparently overwinters as pupae inside the gall. The adults reared from screened galls emerged in February, just when goldenrod seedlings were ready to come up. No parasites were reared from this gall.

The last and rarest gall collected is made on the roots by Diapriids prob. Agathidium (Olsen.). The large white nodule develops inside an elliptical, potato-like gall on the rhizomes of Solidago Canadensis (Fig. 5.3). No adults of this species were obtained.

The leaf mines of the Braconitidae moth, Conostigmotoma galligena Frey and Hoff. (previously placed in the genus Stenocolligata), were very common on the underside of leaves of S. canadensis, S. flexilis, and S. rigida. They were found from early May to early October in Gainesville. The tiny larva made an irregular, roundish blotch, usually centered, on the underside of the leaves. As the larva grew the mine became elongate. By pupation, the leaf was folded in the damaged region and the mine became whitish. The elongate, white mine in which the larva pupated was suspended inside the fold by silken threads. This is a common species in the United States (Brown, 1938).

Agapostola solidaginisella is a Tenthredinid moth whose larvae feed in the growing tips or mine the leaves of various species of Solidago (Brown, 1932). Only pupae and adults of this species have been collected in this study, on the leaves of Solidago canadensis.

The bright, yellowish larvae of Aspilota fumifera Frey (Hymenoptera) were well concealed on the flower heads of S. flexilis, where they fed on the seeds. Adults of this species appear from late July to late

September in central and eastern U.S. (Parker, 1948). In this study, no adults were collected and the larvae were observed in October and early November.

The jumping plant-lice Cassidulopharyngia spazi (Pavani) has been reported from Salicage sp. (Calwell, 1938) and Aster (Crawford, 1934). In Salicaville, adults were occasionally collected on leaves of L. filiculme and L. grandifolia, from July to November.

The Beneficial Fauna

The beneficial fauna associated with goldenrod in Salicaville were represented by 123 species of entomophagous arthropods and 38 species of pollinators (Table 3). Among the entomophagous species, 44% were predators, including two species of fungus feeders, and 56% were parasitoids. The 44 species of predators were distributed among eight orders and 26 families of insects, eight families of spiders and one family of Opiliones. The spiders represented 54% of the predators, but 26 of the 64 species were rare, i.e., collected only once in three years of study. The population of the common spiders (collected at least in 60% of the samples) and of the occasional ones (present more than once in 4 green plant species) fluctuated during the year, with 14 species present the whole season, five species present only in spring (April to July), and five species restricted to the blooming season (July to October). Halfen of these spiders bred on goldenrod. The green lynx, Spizella glidatus (Pavani) was the most abundant spider throughout the year, collected from April to November on all four species of goldenrod studied. This species breeds late in the season, when goldenrods were blooming. In 1948, it was so abundant in one population of Salicage filiculme that almost every plant had one green lynx attending its egg

Table 1, continued

McCluskey-type

<u>Polynomial, identifier</u> (page, line)	Φ	L_A	P	$h_{\Phi}M$
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Article 100

<u>Equation (1) (page 100, line 10)</u>	B	A	Pr	h_1
<u>Equation (2) (page 100, line 11)</u>	C	L_A	Pr	h_1, h_2, h_3, h_4
<u>Equation (3) (page 100, line 12)</u>	C	L_A	Pr	h_1, h_2, h_3, h_4
<u>Equation (4) (page 100, line 13)</u>	B	A	Pr	h_1, h_2
<u>Equation (5) (page 100, line 14)</u>	B	A	Pr	h_1
<u>Equation (6) (page 100, line 15)</u>	C	L_A	Pr	h_1, h_2, h_3, h_4
<u>Equation (7) (page 100, line 16)</u>	B	A	Pr	h_1
<u>Equation (8) (page 100, line 17)</u>	C	A	Pr	h_1, h_2
<u>Equation (9) (page 100, line 18)</u>	B	L_A	Pr	h_1, h_2
<u>Equation (10) (page 100, line 19)</u>	C	L_A	Pr	h_1, h_2, h_3, h_4
<u>Equation (11) (page 100, line 20)</u>	B	A	Pr	h_1

Article 101

<u>Equation (1) (page 101, line 10)</u>	B	A	Pr	h_1, h_2
<u>Equation (2) (page 101, line 11)</u>	B	A	Pr	h_1
<u>Equation (3) (page 101, line 12)</u>	B	A	Pr	h_1
<u>Equation (4) (page 101, line 13)</u>	B	A	Pr	h_1, h_2, h_3

Theorem 102

<u>Equation (1) (page 102, line 10)</u>	B	L_A	Pr	h_1, h_2
<u>Equation (2) (page 102, line 11)</u>	C	L_A	Pr	h_1, h_2, h_3
<u>Equation (3) (page 102, line 12)</u>	B	A	Pr	h_1
<u>Equation (4) (page 102, line 13)</u>	B	A	Pr	h_1
<u>Equation (5) (page 102, line 14)</u>	C	L_A	Pr	h_1, h_2

Article 103

Theorem 103

<u>Equation (1) (page 103, line 10)</u>	C	A	Pr	h_1, h_2, h_3, h_4
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Table 3, continued

Scaphiops

<u>Scaphiops</u> sp. 1	B	A	Pr	Sr	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> sp. 2	B	L	Pr	Sr	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> sp. 3	B	L	Pr	Sr	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> sp. 4	B	L, P	Pr	Sr	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)

Tegulops

<u>Tegulops</u> <u>Scaphiops</u> (Faint)	B	A	Pr	Sr	
<u>Tegulops</u> <u>Scaphiops</u> (Faint)	B	A	Pr	Sr	
<u>Tegulops</u> <u>Scaphiops</u> (Faint)	B	A	Pr	Sr	

Gastropods

Cancellaria

<u>Cancellaria</u> <u>Scaphiops</u> (Faint)	C	L, A	Pr, Pt	Sr, Pt, Ag, Pt	
<u>Cancellaria</u> <u>Scaphiops</u> (Faint)	C	A	Pr	Sr, Pt, Pt	

Scaphiops

<u>Scaphiops</u> sp. 1	B	A	Pr	Sr	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> sp. 2	C	L, A, B	Pr	Sr, Pt, Ag, Pt	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> <u>Scaphiops</u> (Faint)	B	A	Pr	Sr, Pt	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> <u>Scaphiops</u> (Faint)	B	A	Pr	Sr	D ₁ - <u>Scaphiops</u> D ₂ - <u>Scaphiops</u> (Faint)
<u>Scaphiops</u> sp.	B	A	Pr	Sr, Pt	Faint

Table 2, continued

<u>Species name</u> , <u>loc.</u>	<u>C</u>	<u>L.A</u>	<u>Fr</u>	<u>Se,Fl,St</u>	<u>St. (seeds only)</u> <u>St. (fruits)</u> <u>Seeds</u>
<u>Leguminosae</u>					
<u>Clitoria</u> , <u>sp.</u>	0	A	Fr	St,Fl	
<u>Labiales</u>					
<u>Polypogon</u> , <u>sp.</u>	0	L.A	Fr	St,Fl	Seeds
<u>Myrtaceae</u>					
<u>Elaeagnus</u> , <u>sp.</u>	0	A	Fr	St	Seeds in Fruits
<u>Convolvulaceae</u>					
<u>Convolvulus</u> , <u>sp.</u>	0	A	Fr	St	
<u>Convolvulus</u> , <u>sp.</u>	0	A	Fr	St	
<u>Convolvulus</u> , <u>sp.</u>	0	A	Fr	St,Fl	Seeds in Fruits
<u>Urticaceae</u>					
<u>Urtica</u> , <u>sp.</u>	0	A	Fr	St	
<u>Peridoreae</u>					
<u>Peridoreae</u> , <u>sp.</u>	0	L.A	Fr	St	
<u>Peridoreae</u> , <u>sp.</u>	0	A	Fr	St,Fl	
<u>Peridoreae</u> , <u>sp.</u>	0	A	Fr	St,Fl	
<u>Myrtaceae</u>					
<u>Myrtaceae</u> , <u>sp.</u>	0	L.A	Fr	St,Fl,St	Seeds in Fruits

Table 3, continued

Isosurfaces					
<u>Asymptotic</u> α_0	4	1	β_0	β_0	1. <u>Asymptotic</u> α_0 (1970-1971)
<u>Collapsing</u> α_0	0	1	β_0	β_0, β_1^*	1. <u>Collapsing</u> α_0 (1970-1971) 2. <u>Collapsing</u> β_0, β_1^* (1970-1971)
<u>Collapsing</u> α_0	0	1	β_0	β_0	2. <u>Collapsing</u> β_0, β_1^* (1970-1971)
<u>Extrapolation</u> α_0 - <u>Asymptotic</u>	0	1	β_0	β_0	2. <u>Extrapolation</u> α_0 (1970-1971)
<u>Asymptotic</u> α_0 - <u>Collapsing</u> α_0	4	1	β_0	β_0	2. <u>Asymptotic</u> α_0 (1970-1971)
<u>Collapsing</u> α_0 - <u>Collapsing</u> α_0	0	1	β_0	$\beta_0, \beta_1^*, \beta_2, \beta_3$	(Asymptotic) <u>Collapsing</u> α_0
<u>Collapsing</u> α_0 - <u>Collapsing</u> α_0	0	1	β_0	$\beta_0, \beta_1^*, \beta_2, \beta_3$	(Asymptotic) <u>Collapsing</u> α_0
<u>Extrapolation</u> α_0 - <u>Extrapolation</u> α_0	0	1	β_0	β_0	(Asymptotic) <u>Extrapolation</u> α_0
<u>Extrapolation</u> α_0 - <u>Extrapolation</u> α_0	0	1	β_0	$\beta_0, \beta_1^*, \beta_2, \beta_3$	2. <u>Extrapolation</u> α_0 (1970-1971)
<u>Extrapolation</u> α_0 - <u>Extrapolation</u> α_0	0	1	β_0	β_0, β_1^*	2. <u>Extrapolation</u> α_0 (1970-1971)
Other cases					
<u>Extrapolation</u> α_0 - <u>Extrapolation</u> α_0	0	1	β_0, β_1^*	β_0	<u>Extrapolation</u> α_0 (1970-1971)
Refutation					
<u>Collapsing</u> α_0	0	1	β_0	β_0	
Asymptotic					
<u>Asymptotic</u> α_0	0	1	β_0	β_0, β_1^*	2. <u>Asymptotic</u> α_0 (1970-1971)
Extrapolation					
<u>Extrapolation</u> α_0	0	1	β_0	β_0, β_1^*	(Asymptotic) <u>Extrapolation</u> α_0
Extrapolation					
<u>Extrapolation</u> α_0 - <u>Extrapolation</u> α_0	0	1	β_0	β_0	1. <u>Extrapolation</u> α_0 (1970-1971)

Table 2, continued

Reflexion					
<u>Amphibolite, matrix</u> <u>epitaxial</u>	0	4	Pr	Sc	
<u>Metabas. (basalt) Gr</u>	0	4	Pr	Sc	
Intergrowth					
<u>Troxolite, hornblende (basalt)</u>	0	1	Pr	Sc, Sr	1. <u>hornblende</u> <u>(Pr+Sr)</u>
Regional lens					
<u>Basalt Gr. 10-</u>	0	0	Pr	Sc	Lepidolite
Metallite					
<u>Basaltite, 10- (epitaxial)</u> <u>[11]</u>	0	4	Pr	Sc	Gr. [1]
Spectro					
<u>Basaltite, 10- (epitaxial)</u>	0	1	Pr	Sr	1. <u>10- 10-</u> <u>epitaxial</u> <u>(Pr+Sr)</u>
<u>Basaltite, matrix (basalt)</u>	0	1	Pr	Sc, Sr, Pr, Sr	2. <u>epitaxial, 10- 10-</u> <u>(Pr+Sr)</u>
<u>Basalt, 10-</u>	0	1	Pr	Sc	3. <u>epitaxial</u> <u>(Pr+Sr)</u>
Placed lens					
<u>Epitaxial, 10-</u>	0	1	Pr	Sr	4. <u>epitaxial</u> <u>(Pr+Sr)</u>
<u>Epitaxial, 10-</u>	0	1	Pr	Sc	5. <u>epitaxial</u> <u>(Pr+Sr)</u>
<u>Epitaxial, 10- 1</u>	0	1	Pr	Sc	6. <u>epitaxial</u> <u>(Pr+Sr)</u>
<u>Epitaxial, 10- 2</u>	0	1	Pr	Sc	7. <u>epitaxial</u> <u>(Pr+Sr)</u>
Good looking					
<u>Epitaxial, 10-</u>	0	1	Pr	Sr	

Table 3, continued

Reproductive					
<u>Marbled murrelet</u> (Puffin)	E	P	Pr	Sc	
Non-reproductive					
<u>Red-tailed tropicbird</u> (Tyr)	E	L	Sc	Pr	Spiders = egg mass spiders
<u>Red-tailed tropicbird</u> (Tyr)	E	L	Sc	Pr	
Overlapping					
Parasitizing					
<u>Red-spotted cuckoo</u> (Cuck)	E	L	Pr	Sc	
Overlapping					
Parasitizing					
<u>Red-spotted cuckoo</u> (Cuck)	E	L	Pr	Sc	
Overlapping					
Parasitizing					
<u>Red-spotted cuckoo</u> (Cuck)	E	L	Pr	Sc	

E = eggs, L = larvae, P = pupae, Pr = pupae, Sc = adults

E = eggs, L = larvae, P = pupae, Pr = pupae, Sc = adults

Pr = parasitoid, Pa = parasitoid, Pr = parasitoid

Sc = Scorpaenidae, Pr = Prionidae, Pa = Paenidae, Pr = Prionidae, Pr = Prionidae

*Not listed by name as a pest

disturbed. This situation compares to that of the unstable agroecosystem, where a natural balance between prey and natural enemies rarely occurs. A comparative analysis of the entomofauna of each goldenrod species could better explain the relationships existing between the phytophagous and the entomophagous fauna associated with this plant. The goldenrod populations surveyed in this study grew in different situations, with variable degrees of human interference. More disturbed environments would be expected to have a more unbalanced fauna than stable, more natural environments.

Of the 20 species of pollinators, 15 were hymenoptera and 12 were lepidoptera. Most of the latter, however, were rare. Only *Clitella fulvicollis* (Walker) (Doleridae) and *Clithra tarsata* (Cresson) (Noctuidae) were occasional. The most common pollinators were the honeybees (*Apis mellifera* L.), the bumble bee (*Bombus terrestris* L.), and the solitary bees (*Osmia lignaria* Say). In this sequence. Nonetheless, solitary bees and syrphid flies have been reported as major pollinators of *S. canadensis* in Canada and Michigan (Warner et al., 1980). Only one species of aphid was collected visiting flowers of goldenrod in Delaware. The bumble bee was very abundant and seemed to prefer the goldenrod flowers among the other blooming plants.

The guild distribution of the insect fauna on the four species of goldenrods in Delaware is shown in Fig. 4. The phytophagous fauna was dominated by the sap feeding insects. Only one of them is apparently specific to *Solidago* and was found on the plant. The chewers were the next most abundant group followed by the gall makers, leaf miners and beetles.



Figure 4. Spatial distribution of the 125 species of insects associated with *Salix sp.* in Sakrebulo. The phytophagous fauna comprising 113 species is shown hatched.

Predators represented the largest group, and their population did not oscillate much during the year (Fig. 5), even when the phytophagous population was going down. This may be related to the presence of aphids on the plant throughout the growing season. The most abundant predators, the green lace, lady beetles and lacewing larvae are aphid feeders. In the absence of the preferred prey the aphids could serve as alternate prey to the other predators.

The predator population peaked in July and then stabilized before crashing in November. The parasitism, the third largest group (Fig. 4) peaked in May (Fig. 5) and slowly decreased as the season progressed. Most most of the parasitism represented in this study were reared from leaf feeding insects, the pattern of their curve in Fig. 5 may represent that of their hosts. As the leaves get old they become less palatable and nutritious to the insects. Any reduction in the population of leaf feeders would result in a consequent reduction in the population of their parasitism. The relationship between seasonal changes in the arthropod community and the changes in the complexity of the host plant will be discussed further.

Several ants were collected on goldenrods during this four year study. Some of them were feeding aphids, and many were predators. The most common species was Camponotus caryocarpus (Linn.) followed by Formica ruginodis (F.) and Formica ruginodis (F.). Nests of the latter were found in dried goldenrod stems in the winter. Following is a list of the 34 species collected. The species Myrmica ruginodis is a new state record.

Camponotus caryocarpus (Linn.)

Camponotus floridanus (Ruckw.)

Cardiomyrma ruginodis (F.)

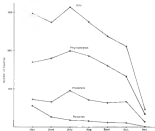


Figure 5. Seasonal distribution of parasitoids, predators, phytophagous and total insect faunas associated with four species of gall-formers in Galesos (Ile).

Leptocordulia virgatula (Forsk.)

Emergence 14.

Emergence Chrysopa 14th

Emergence Chrysopa 14th

Emergence Chrysopa 14th

Emergence Chrysopa 14th

Emergence 14.

Emergence Chrysopa 14th

Emergence Chrysopa 14th

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Emergence Chrysopa 14th

Emergence Chrysopa 14th

Emergence Chrysopa 14th

Emergence Chrysopa 14th

Final Suitability of Chrysopa 14th for Chrysopa 14th

Larval and Adult Performance

Eggs of Chrysopa 14th in the laboratory took four to five days to hatch. Larval developmental time was consistently longer for males than for females larvae and it varied significantly depending on the preferred species on which they fed (Table 4). Males and females reared on Chrysopa 14th developed faster, in both the 1980 and 1981 experiments, than

TABLE 4.—Developmental time from hatching to pupation, number of adults emerged, and weight of newly emerged adults of *Spargania tuberosa* fed with each of the host species. Values are average number \pm standard deviation.

Host Plant	Developmental Time (Days)						No. Emerged		Weight, mg ²	
	1960						1961	1962	1961	1962
	Days	Pupa to	Days	Pupa to	Days	Pupa to				
B. <i>transversalis</i>	25.7 \pm 0.56 ²	21.3 \pm 0.46	(20)	16.3 \pm 0.36	(20)	21.3 \pm 0.46	5	40	2.0 \pm 0.26	1.7 \pm 0.26
	(10)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(20)	(20)
B. <i>crucifera</i>	17.7 \pm 0.46	16.3 \pm 0.36	(11)	15.3 \pm 0.36	(10)	15.3 \pm 0.36	20	18	2.0 \pm 0.46	16.3 \pm 0.36
	(11)	(11)	(11)	(10)	(10)	(10)	(20)	(20)	(20)	(20)
B. <i>flavipes</i>	20.2 \pm 0.36	16.3 \pm 0.36	(21)	16.3 \pm 0.36	(21)	17.3 \pm 0.36	8	1	2.0 \pm 0.36	1.7 \pm 0.36
	(20)	(21)	(21)	(21)	(21)	(21)	(20)	(20)	(21)	(21)
B. <i>truncatellus</i>	26.3 \pm 0.36	20.3 \pm 0.36	(11)	16.3 \pm 0.36	(12)	16.3 \pm 0.36	8	4	2.0 \pm 0.46	16.3 \pm 0.36
	(11)	(11)	(11)	(12)	(12)	(12)	(20)	(20)	(20)	(20)

²Values within a column followed by the same number are not significantly different at the 5% level by Student's *t*-test. Lower subscripts indicate the number of samples taken.

Numbers in parentheses indicate the sample sizes.

Average weights obtained in 1961 and 1962 together, with the description of female weights as B. *flavipes*, which is the average value of 1962 only.

on any of the other hosts. The only two families reared on *L. glaberr* had the same average developmental time as families reared on *L. fuscipes*, but this may be a result of the small number of observations on the former. Moles reared on *L. lanceum* took the longest to develop, but not significantly longer than moles reared on *L. glaberr*. There was no difference among developmental time of moles, in 1963, and of families in 1964, fed with *L. grandis* var. *gigantea* and *L. glaberr*.

Survivorship was also significantly higher on *L. fuscipes* in both years (Table 4). In 1963, the number of survivors in the other three plant species was not significantly different from each other. In 1964, however, survivorship was considerably higher on *L. grandis* than on *L. glaberr* and *L. lanceum*.

Females developed faster, and were heavier at emergence than males ($t = -3.68$, $P < 0.005$). The influence of the host plant on the weight of newly emerged adults was not very clear. Females were heavier when fed with *L. fuscipes* although their mean weight was not significantly higher than that of females fed with *L. lanceum*, which in turn did not differ from females on the other 2 hosts. Moles reared on *L. fuscipes* were also heavier, although not significantly more than moles reared on *L. grandis*. The lightest moles were those from *L. lanceum*, followed by those from *L. gigantea* (Table 5).

Adult performance, based on fecundity and longevity, could not be measured on *L. glaberr* in 1963 or on *L. gigantea* and *L. lanceum* in 1964 due to the small number of reared adults and to their death soon after emergence. The average number of eggs/fecundity on *L. fuscipes*, although not statistically significant, was considerably higher than that of *L. lanceum* in 1963 and was significantly higher than the average

egg production per day by females reared on *E. canadensis* in both years (Table 5). Longevity was approximately the same for males and females and did not statistically differ among the three treatments (Table 5) in 1983. In 1984, however, the life span of adults fed with *E. fistulosae* was significantly higher than that of adults fed with *E. canadensis*.
Nitrogen and Water Content of Leaves

Although the variation in water content among the four polycross species was small (48-51 to 75-78, Table 6), the mean water content of the leaves of *E. canadensis* and *E. fistulosae* was significantly higher than that of *E. gigantea* and *E. laevigata*. Nitrogen content, on the other hand, was lower in *E. canadensis* than in the other three plant species. Better performance was obtained by insects reared on *E. fistulosae*, the most nutritious host in terms of both water and nitrogen content. Apparently, the low nitrogen content of the leaves of *E. gigantea* and *E. laevigata* had a significant effect on the development and reproduction of *E. laeta*, because its performance was not that predicted by the leaf nitrogen content. For example, the correlation coefficient between number of eggs laid/female/day and leaf nitrogen in 1983 was not significant ($r = 0.048$, $p = 0.18$, Table 7). This analysis included *E. canadensis*, *E. fistulosae* and *E. laevigata*. There are no fecundity data for *E. laevigata* in 1984 and the correlation coefficient analysis of 1984 year included only *E. fistulosae* and *E. canadensis*, both with high leaf water but significantly different in leaf nitrogen. This time the linear relationship was significant (Table 7). The same result was obtained for life span (Table 7).

Table 1. Number of eggs/female/day and 10th roots of males and females of coarcted *Adactynella* (average for each host species). Numbers are average \pm standard deviation.

Host Plant	No. of eggs/female/day		10th roots of males and females (mm)	
	Leaf	Leaf ²	Leaf	Leaf ²
<i>A. clausenii</i>	5.83 \pm 2.15 ^a (10)	5.97 \pm 1.87 (10)	64.25 \pm 12.05 ^a (4)	62.04 \pm 18.30
<i>A. filiformis</i>	6.39 \pm 2.05 ^a (10)	6.41 \pm 2.5 (10)	63.46 \pm 12.15 ^a (10)	65.36 \pm 25.47
<i>A. haemorrhoidalis</i>	3.48 \pm 1.41 ^a (6)	-	42.403 \pm 18.35 ^a (10)	-

^aValues are statistically different at 10 level by a test.

Values within a column followed by the same letter are not significantly different at the 10 level by Scheffé's with Student modification for unequal sample sizes.

Numbers in parentheses indicate the numbers observed.

Table 4. Water and nitrogen content of leaves of four plants fed to larvae and adults of *Sphrecilla* (colony). Sample sizes are 3 and 14 for water and nitrogen content, respectively.

Plant Species	Water Content (% of fresh wt.)	Nitrogen Content (% of dry wt.)
<i>E. canadensis</i>	76.08 \pm 3.9 ^a	1.93 \pm 0.10b
<i>E. fistulosus</i>	74.76 \pm 3.3a	2.40 \pm 0.30a
<i>E. glaucus</i>	69.40 \pm 3.7b	2.50 \pm 0.20a
<i>E. leavenworthii</i>	68.81 \pm 4.0b	2.31 \pm 0.20a

^aMeans within a column followed by the same letter are not significantly different at the 5% level by Duncan's Multiple Range Test.

Table 2. Correlations of larval and adult performance with leaf water and nitrogen content. Each sample set of the dependent variable was correlated with the mean value of the independent variable.

Dependent Variable	Year	Independent Variable	
		Leaf Nitrogen	Leaf Water
---Correlation Coefficients---			
Bio. developm., time	1943	-0.387	-0.521**
Bio. developm., time	1944	-0.393***	-0.392**
Family developm., time	1943	-0.339*	-0.381
Family developm., time	1944	-0.543***	-0.359**
No. adults emerged	1943	0.179	0.303
No. adults emerged	1944	-0.131	0.362***
Bio. weight	1943 & 1944	0.043	0.133
Family weight	1943 & 1944	0.116	0.132
Eggs/female/day	1943	0.365	0.045
Eggs/female/day	1944	0.313***	0.313
Adult life span	1943	0.019	0.079
Adult life span	1944	0.354***	

P_1 , etc., are, one deviation coefficient significant at 1%, 5%, 1%, 5%, and 1% levels, respectively.

Oviposition and Feeding Preference

Given a choice among the four host plants for oviposition, the females tended to prefer L. foeniculacea and L. canadensis. This preference, however, was not statistically significant. There was a slight tendency by adults to oviposit on their original host plant by females reared on L. filifolius and L. canadensis. Females reared on L. glauca and L. lanceolatifolia, however, apparently distributed against their original hosts, as they never chose this plant for oviposition. A similar trend for feeding preference was observed although the differences among treatments were even smaller than those for oviposition and the adults reared on L. glauca and L. lanceolatifolia did not clearly avoid their original hosts (Table 4).

The chrysomelid beetle, Sphenella integra (LeConte) originally in the genus Salicaria, was moved in 1883 to the genus Salicicollis by Horn. In 1885, Wilcox described the new genus, Sphenella, composed of three species, four of which are specific feeders on Salicagae spp. (Woods, 1984; Wilcox, 1985). S. integra is reported from blue anemone, Opuntia polyloba, of the family Lythraceae, by Wilcox (1985). This record apparently originated from Halsebaugh and Hays (1931) who reported that the adults of this beetle "were collected by a home gardener on a plant he called 'anemone' (Opuntia polyloba)?". This does not seem to be a very reliable record. Salicagae, and not Opuntia, appears to be the true host plant of S. integra, since most of the other Sphenella species are restricted to one host genus, and many of them feed on plants of the family Compositae.

This beetle is reported from Pennsylvania, Florida, Texas (Wilcox, 1985) and Alabama (Halsebaugh and Hays, 1931). In Salicicollis, it occurs

Table 8. Best choices for feeding and prioritization of males and females at *Sperdella* colonies. The values represent the number of times the insect chose that best option.

Original host	Sample 21a		Sample 21b		Sample 21c		Sample 21d		Sample 21e		Sample 21f		Sample 21g		Sample 21h		Sample 21i		Sample 21j		Sample 21k		Sample 21l	
	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.	Food	Grp.
<i>S. caudata</i>	36	26	33	7	7	3	18	3	3	3	18	3	3	3	3	3	3	3	3	3	3	3	3	3
<i>S. floricola</i>	44	14	33	4	18	8	7	1	6	8	7	1	6	8	7	1	6	8	7	1	6	8	7	1
<i>S. glaucus</i>	31	8	26	1	30	4	7	0	4	3	30	4	7	0	4	3	30	4	7	0	4	3	30	4
<i>S. immutabilis</i>	20	8	31	3	30	3	8	3	3	3	30	3	8	3	3	3	30	3	8	3	3	3	30	3

The descriptive tables best choices for feeding and prioritizing were not significant at 16 tests by χ^2 test.

on the four common species of Salicaceae: S. amygdaloides var. glabra (= S. alba), S. flabellata, S. glauca and S. lasiolepis. Both larvae and adults feed on leaves. Females appear in the field in early May. They lay a clutch of conspicuous, orange eggs on the underside of the leaf. The clutch size in the field is almost always six eggs with usually not more than one clutch per plant. Young larvae move upward and feed on the new leaves. There are three larval instars. The first two instars feed up mineralizing the leaf. Third instar larvae eat elliptical holes in the leaf blade. Prior to pupation the third instar larva spins a loose net-like cocoon composed of a silken matrix secretion. In the laboratory, the prepupa searches for corners or folds on the leaf and thins paper beside the covering up where it pupates. No pupa was found on plants in the field. These observations suggest that S. integris, like other species of this genus (Woods, 1974), pupates in the soil.

Eggs of this species were seen on plants in the field as late as the early October in Silverville. Adults and larvae may be collected until early November. Developmental time in the laboratory, from hatching to adult, averages 27 days. Since goldenrod stands dry down to almost early winter, the occurrence of larvae in the field until early November suggests that this species overwinters not only as adults like other Sparganiid beetles (Woods, 1974) but also as pupae, in the soil. Adults were seen on S. flabellata early in May and one week later they were seen on S. amygdaloides. A few adults could be collected on S. glauca and S. lasiolepis late in May and the beginning of June, respectively. They were very scarce on the latter. In the laboratory survivorship of larvae and adults on these latter two species was very low with few individuals

reaching adulthood. Those fed B. glaucus that did survive to the adult stage had a very short life span (< 10 days).

Several studies have shown the influence of leaf water and nitrogen on insect performance (McNeil and Southwood, 1978; Mattson, 1980; Scriber and Slansky, 1981; Scriber, 1983). Folsa (1977) showed that fecundity, longevity and weight of the western beetle Pissodes valisugatus Fabricius was higher when the insects was fed a host with higher levels of leaf nitrogen. Leaf water content is another factor determining plant quality (Jander, 1977; Scriber and Feary, 1979; Scriber and Slansky, 1981). Better performance is achieved by pseudotsugae leafhopper larvae feeding on hosts which have high leaf water (70% to 85%), as opposed to insects feeding on hosts with leaf water less than 70% (Scriber and Slansky, 1981). Low water content may also have an effect on nitrogen utilization by insects. Larvae of the tortricid moth Hydropsyche caryocopa fed with leaves of low leaf water content grew more slowly and utilized plant biomass, energy, and nitrogen less efficiently, although fiber, total nitrogen and caloric content of these leaves did not differ (Scriber, 1981). When water is not a limiting factor some insects such as Pieris rapae L. (Slansky and Feary, 1983) optimize nitrogen assimilation by altering consumption rate in response to changes in leaf nitrogen content. But when water is apparently limiting nitrogen assimilation efficiency and nitrogen accumulation rate, high feeding rates would not result in faster growth (Scriber, 1977). This seems to be the case for B. latreus whose performance on B. canadensis, which contains low leaf nitrogen but high leaf water did not differ from its performance on B. glaucus. In some instances its performance on B. canadensis was better than that on B. laricina. Both B. glaucus and B. laricina had

higher leaf nitrogen and lower leaf water contents than *S. lamellaria* (leaf water content on *S. lauraster* was even lower than on *S. gigantea*). Indeed, leaf water content of the larvae of *S. gigantea* and *S. lauraster* was lower than that of many other furts (Grier and Faeg, 1974). Larvae and adults of *S. integra* are external feeders and thus may be more susceptible to changes in humidity. Southwood (1977) discussed low leaf water content as a major evolutionary 'barrier' for phytophagous insects, even in the presence of the many physiological, behavioral and ecological adaptations to avoid water loss.

The toxic effects of allelochemicals cannot be excluded as part of the explanation of the residual variation in the relationships between leaf nitrogen and water contents and *S. integra* performance. Several allelochemicals such as terpenes, glycosides and flavonoids have been isolated from galled plants (Miller et al., 1976, 1980; Gundersen et al., 1979; Sauer et al., 1981). These allelochemicals may interfere with an insect's metabolism in such a way that its performance will be less than that expected by leaf water and nitrogen. This was the case in the southern sawfly *Proterops arctica* (Hraser) whose growth response to leaf water and nitrogen was altered by various allelochemicals present in the 18 lupine species in which the larvae were fed (Scriber, 1984).

Males of *S. integra* were not as successful as females, which managed to compensate for the nutrient deficiencies and attain an average weight close to that of females reared on *S. fistulosa*, the most nutritious host. Compared to males, females either consumed food at a faster rate and/or utilized their food more efficiently because they gained more weight in a shorter time. Females accumulate much of the nutrients and energy provided to eggs during their larval development. For this reason

they are heavier than males and usually have longer developmental times. The adaptive significance of the unusually later emergence of males of *B. litigae* may relate to the fact that females are not ready for egg laying until ten to four days after emergence. If male and female emergence was synchronous, the males would be exposed to natural enemies and to environmental hazards while waiting for the females to mature. This could increase male mortality and the females might have trouble finding a mate. Those males that emerged later than the females, however, would be more successful in mating and reproducing. Late male emergence may have evolved in the population in this manner.

Survivorship and fecundity were higher on *Solidago rigida* than on *B. litigae*. Thus it can be inferred that individuals of *B. litigae* that feed on this particular host species have greater fitness. It would therefore be expected that, given a choice among the four goldenrod plants, males and females would preferentially feed on *B. rigida* and females would select this host species for oviposition. This was not the case, perhaps because the plants are very closely related to each other and the insects cannot discern among them before actually "tasting" them. Once they are on a plant they may stay there. In general, females laid their eggs on the plant species on which they were feeding. Host choices by *B. litigae* would be better understood with a knowledge of their dispersal behavior. When disturbed in the field or in the laboratory, *B. litigae* does not fly but falls to the soil and plays dead. Studies on the dispersal behavior of two other beetles of the subfamily Siliandinae, *Chrysobothris viridis* LeConte and *Chrysobothris harrisii* Fiske (Reeside, 1933) demonstrated that these beetles exhibit the segmentally-flipped syndrome, flying only during a semi-teneral but pre-reproductive phase. They perform long-range

dispersal and colonization of other fields only at this time. This may very well be the case with B. integris. The goldenrod fields, as indicated, are generally composed of only one species. Once the beetles, on its pre-dispersal flight reached this field, its dispersal may become restricted to walking movements from plant to plant, because the feeding and oviposition experiments were performed using ovipositing females, their stimulus for host selection may have already been blocked. They probably were not able to emit a "strong response" and were simply ovipositing on whatever plant they were on at the time. Field studies on dispersal behavior are necessary for a better understanding of the mechanism of host choice and host selection of B. integris.

Host Specificity of Leptogaster sp. for
Scirpus spp. in the Field

B. integris was the only species of Leptogaster collected as goldenrods in Grassville, although 4 other species of this genus feed on goldenrod. Three of these other species are polyphagous, but B. pallens Freeman (Hoffer and Harris, unpublished data) and B. distincta have been reported only from Leptogaster.

Larvae of B. distincta were collected in Grassville from early May to the beginning of September. An egg mass collected in the field was found over the vein vein on the underside of the leaf. In the laboratory, females laid eggs indiscriminately on either side of the leaf or on cage walls. Each egg mass contained 25.0 ± 11.8 greenish, transparent, circular to oval shaped eggs. They gradually turn yellowish and then reddishbrown as the embryo develops. Under laboratory conditions, the eggs took 3 to 7 days to hatch.

Despite eggs being laid in masses, more than one larva per plant was rarely seen in the field. The active newly hatched larvae probably dispersed by spinning silk threads on which they suspended themselves and moved from the egg mass site to other plants. Late instar larvae were never observed suspended on silk threads.

Seven parasitic Hymenoptera were reared from larvae of *L. distincta*, including five braconids (*Chorebus* sp., *Ichneumon* sp., *Microgaster* sp., *Pimpla* sp. 1 and *Pimpla* sp. 2), 1 ichneumonid (*Microctonus* *fluctivorus* Ashmead) and 1 ichneumonid (*Chasmodon ferrugineus* (Morton)). The most common species was *Pimpla* sp. 1.

Development and fecundity of *L. distincta* reared on the four common species of goldenrod in Salverville are presented on Table 8. The average male developmental time from hatching to pupae ranged from 21.8 to 24.4 days, depending on the host plant they were fed on. It was a little shorter than average female developmental time which ranged from 22.4 to 25.4. The variation within a given sex is apparently related to the nutritional quality of the food. Analysis of leaf water and nitrogen content of the four goldenrod species used in this study are presented in Table 8. Developmental time of male and female was significantly shorter on *L. glaberrima*, the plant with the highest leaf water and nitrogen content. Larvae reared on *L. canadensis* var. *major*, the host with significantly lowest leaf nitrogen took the longest time to develop, but the difference in developmental time on this species and on *L. glaberrima* and *L. latifolius* was not statistically significant. These results are in agreement with those observed for the beetle *Epuraella lugens* (Gyllenhal) in the previous chapter. The low leaf water content of the two taller plant species may have limited nitrogen assimilation efficiency

Table 8. Larval and adult performance of *Conopsea* spp. on the four host plant species. Means are average \pm standard deviations, with n number of the number of plants analyzed.

Host Plant	Experimental Fly Size Mean \pm S.D. (mm)		Food Intake (mg)		Number of Adults (Survived)	Survival (%)	Larval Size (mm)
	Male	Female	Male	Female			
<i>C. conopsea</i>	26.1 \pm 3.4 (2) (10)	26.6 \pm 2.8 (6) (10)	2.4 \pm 0.4 (6) (10)	3.4 \pm 0.1 (6) (10)	16	100	4.3 \pm 3.7 (6) (10)
<i>C. chrysanthi</i>	25.4 \pm 3.4 (6) (10)	27.0 \pm 1.4 (6) (10)	3.8 \pm 3.4 (6) (10)	3.3 \pm 0.3 (6) (10)	50	100	3.4 \pm 3.3 (6) (10)
<i>C. clausenae</i>	26.3 \pm 3.4 (6) (10)	26.3 \pm 2.7 (6) (10)	2.3 \pm 3.3 (6) (10)	3.3 \pm 0.4 (6) (10)	25	100	4.3 \pm 3.3 (6) (10)
<i>C. immutabilis</i>	24.4 \pm 3.3 (6) (10)	25.3 \pm 2.3 (6) (10)	2.3 \pm 3.4 (6) (10)	3.4 \pm 0.4 (6) (10)	25	100	3.3 \pm 3.3 (6) (10)

Plant within a column followed by the same letter are not significantly different at the 5% level. Numbers in parentheses indicate the sample size.

and nitrogen accumulation rate by the larvae. The main effect of low humidity and other factors such as allelochemicals on the nitrogen utilization by insects is discussed by Jarvise (1977). Average developmental time of males and females of *L. dillicata* was inversely correlated with leaf nitrogen content (Fig. 4, a and b). The number of adults reared on each host plant (Fig. 4, c) and the number of eggs laid/female/day (Fig. 4, d) were directly correlated to the amount of this nutrient on the food plant. Leaf water content did not show any direct effect on development, survivorship and fecundity as shown by the low correlation coefficients between this variable and the measures of larval and adult performance ($r = 0.22$ and $r = 0.48$ for male and female developmental time, respectively, $r = -0.1$ for number of adults reared, $r = 0.11$ for number of eggs/female/day. None of the coefficients was significant). Its side effect on survivorship and fecundity was also not apparent, since the number of adults reared and the number of eggs laid/female/day was consistently higher on the hosts with higher leaf nitrogen content, even if the leaf water content was low. *L. dillicata* has a behavioral adaptation to prevent water loss by tying the leaves to each other forming a protective case. Small variations in the moisture content of its diet may not strongly affect its performance.

Although causing an increase in the developmental period of *L. dillicata*, low leaf water and nitrogen did not affect the weight of the pupae. Larvae of *Pieris rapae* adjust their feeding rate to compensate for low nitrogen content on its diet. By increasing their rate of food consumption, they maximize the nitrogen accumulation rate, thus increasing their growth rate (Hansen and Feeny, 1977). The ultimate goal of a larva is to become an adult with high fitness. The weight at

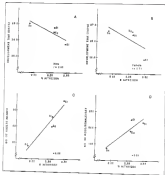


Figure 3. Developmental time of males (A) and females (B) of *Juncos*, number of adults reared (C) and number of eggs per larva (D) in relation to total nitrogen content of the leaves of four species of *Juncos*. $J. o.$ = *J. oreganus*, $J. p.$ = *J. pallasi*, $J. d.$ = *J. dianthus*, $J. l.$ = *J. leucostictus*.

nutrition is an important factor in this fitness and when faced with low nutritional quality of its diet, the larvae may have to eat for a longer period of time to attain some minimal body weight (Glenick, 1982). *L. distalis* grew slower on *L. canadensis*, *L. glauca* and *L. heteromorphus* but attained approximately the same body weight at pupation as on *L. fruticosa*. This did not result in equal fecundity as would be expected. Nelson (1980) reports that heavier or larger adults of insects belonging to several orders, including Lepidoptera, tend to lay more eggs than small ones. Adults of *L. distalis* only feed on nectar, so the energy and nutrients provided to eggs was probably stored during larval development. Although the larvae obtained a minimal body weight at pupation, they did not accumulate enough nutrients to provide for minimal egg production when fed on *L. canadensis*, a nitrogen-deficient host.

Field studies are needed to determine the number of generations a year, the overwintering stage and the mechanisms of dispersal and host selection of *L. distalis*.

Host Architecture and Insect Biology

The architectural complexity of *Lathyrus canadensis*, *L. fruticosa*, *L. glauca* and *L. heteromorphus* were determined by measuring plants at four different growing stages in 1981. Each time the plants were measured, the insect population was surveyed. In 1982 the measurements were repeated on *L. canadensis* and *L. heteromorphus*, this time in three growing stages. The 1980 data were first analyzed separately to detect variations in plant structure among species, locations and months. The three parameters used as determinants of the plant architecture, height of plant, total leaf area (number of leaves x average leaf area) and size of flower stalks (number x average size of flower stalks) were

significantly different among the seven locations and the four months. The interaction between months and locations was also significant (Table A1). These results indicate that location, and not plant species, was the main source of variation. Table 13 shows the interaction means between location and month for height, total leaf area, size of flower stalks, number of phytophagous insect species, number of beneficial species (including insects, spiders and Opiliones), and total number of species.

Results of the statistical analysis of the 1983 and 1984 data confirmed previous results similar to those obtained for 1981 only (Table 11 and A1), with significant interactions between years. Thus only 1983 results were used to further compare location in their species/architecture relationship, since only four locations were surveyed in 1984.

Because of the significant interactions observed among location and month, it was possible to use these two variables as replicates in the correlation coefficients and regression analysis. These tests were applied to determine which characteristics of *Solidago* plants accounted for the richness of the insect fauna associated with them. The following were the parameters included in the total height of the plant, total leaf area, "overall architecture", "partial architecture", leaf nitrogen and leaf water content. The "overall architecture" was calculated by combining height + total leaf area + size of flower stalks. The results were ranked following the criteria in Table A2. Since, unlike the other resources, nectar is produced by the plants basically to attract insects, and only a few species exploit the flowers and seeds of the primarily as

Table 11. Average height of the plants, total leaf area and girth of flower stalks, and number of phyllodes, bracteoles and total rosette perenns collected on 22 August 1966, on four periods of the growing season in 1966. Values are means \pm standard deviation. Sample sizes in brackets.

Plant species	Location	Perenns	Height	Leaf area	Flower stalks	Phyllodes per rosette	Bracteoles per rosette	Total perenns per rosette
1. <i>Stenandrium</i>	B.P. Low	May (20)	10.3 (2.4) 10.0 (2.1) 10.0 (2.0)	200.4 (40.3) 208.4 (40.3) 205.4 (40.3)		20	24	20
		Oct. (20)			10.0 (2.0)	12	8	12
	B.P. High	May (20)	10.3 (2.4) 10.0 (2.1) 10.0 (2.0)	200.4 (40.3) 208.4 (40.3) 205.4 (40.3)		20	24	20
		Oct. (20)			10.0 (2.0)	12	8	12
2. <i>Stenandrium</i>	B.P. Low	May (20)	10.3 (2.4) 10.0 (2.1) 10.0 (2.0)	200.4 (40.3) 208.4 (40.3) 205.4 (40.3)		20	24	20
		Oct. (20)			10.0 (2.0)	12	8	12
	B.P. High	May (20)	10.3 (2.4) 10.0 (2.1) 10.0 (2.0)	200.4 (40.3) 208.4 (40.3) 205.4 (40.3)		20	24	20
		Oct. (20)			10.0 (2.0)	12	8	12

Phyllodes and leaf bases included.

Mean values (means of two heights) selected by the two most robust and significantly different at 5% level by Student's *t*-test (sample sizes 10).

Mean values selected by the two most robust and significantly different at 5% level by Student's *t*-test (sample sizes 10).

a source of food, a 'partial architecture' which included only height and total leaf area was also calculated.

The above distribution of the host plant were tested against the number of phytophagous insect species, the number of beneficial species (parasites and predators, including aphids and Spiliines) and the total number of species (phytophagous and beneficial)(Table A10). The results indicated that total leaf area better explained the diversity of the insect fauna of goldenrods. Height, size of stalks and 'overall architecture' were not linearly related to species richness, except for a negative correlation existing between height of plant and number of beneficial insects. Thus, increasing the architectural complexity of the plant by the addition of flower stalks did not result in an increase in the number of phytophagous insects. Partial architecture was linearly related to the number of phytophagous species ($r = 0.46$, $P = 0.01$), but not to the total number of species. The diversity of goldenrods' phytophagous insect fauna shows a good correlation with total leaf area ($r = 0.55$, $P < 0.0005$). The complexity of the foliage also explained part of the variation in the total number of species associated with these plants ($r = 0.38$, $P = 0.005$)(Fig. 1).

Each location and then each species were next tested for these relationships. Again total leaf area better explained phytophagous and total species richness, but the correlation coefficients were not significant because of the small number of observations (Fig. 8).

The seasonal biology of the phytophagous fauna and of populations of the four species of goldenrods in Danneville are shown in Fig. 2

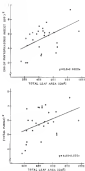


Figure 7. Square root of the number of phytophagous insect species and square root of the total number of species in relation to total leaf area of the host plant ($r = 0.53$ and $r = 0.56$, respectively).

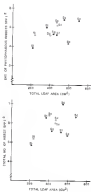


Figure 2. Relationship between total leaf area and the square root of the number of phytophagous insects (a) and to the total number of insects (including aphids) in Lili (○) and Lili (□).

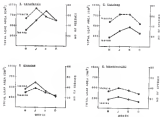


Figure 8. Changes in total leaf area (as a measure of the plant architecture) and in the number of phytophagous insect species in four polynoid species.

lowest for *E. gigantea*, the correlation coefficients between total leaf area (used as a measure of the plant architecture) and the number of phytophagous insects were positively but not significantly linear, perhaps because of the small sample size (mean values of total leaf area and only one insect per month of number of insects). When the four species were analyzed together, the correlation was significant ($r = 0.53$, $P < 0.05$).

The richness of the insect fauna associated with a given plant is a function of several factors, the principal one being the host's geographical range. Plants more widely distributed support higher insect diversity (Strong and Davis, 1988). Within the same geographical range, large, structurally more complex plants are more species-rich than small, structurally simple ones. Plants with the same growth form may still show differences in the insect fauna as a result of local variations in the plant population characteristics, such as height of the plant leaf form and number of related species (Jansen and Price, 1978).

Twenty-three percent of the total number of phytophagous insect species associated with goldenrod in Gainesville were leaf feeders. Thus it is not surprising that the availability of this resource accounted for most of the observed variation in insect species numbers among the collecting sites. Rees and Root (1988) stated that two leaf beetles, *Scirtella caudata* (LeConte) and *Microthripsa vittata* (Fair.) diversified against *Solidago grandifolia* (L.), a distinctive goldenrod with narrow foliage which may be structurally unsuitable for the large black-stems of *S. vittata*. Among the four species of goldenrods in Gainesville there is a gradual variation in leaf form, from the narrow, grass-like leaves of *S. heterophylla* to the larger, wider leaves of *S.*

synanthropic. The number of phytophagous species associated with each host plant in 1988 generally followed this profile, with very few insects collected on L. [arvensis?] compared to the other plant species. The number of insects also followed the seasonal killing of the foliage. Late in the season, when the leaves started to fall, the number of insects dropped, although the overall architectural complexity of the plant increased due to the addition of flower stalks. Thus, increasing the architectural complexity of the plant with flower structures did not result in an increase in the number of insect species. Only two insects that feed on flower and seeds, a weevil with and a ridge, are specific to foliage. Other insects exploiting these structures are polyphagous or feed also on other parts of the plants. Coloured bloom are utilized by different insects and none of them seem to be specific to the plant. Since these plants also reproduce vegetatively by rhizomes, resource allocation to sexual reproduction may vary with age, from year to year and perhaps with environmental conditions. In this sense coloured bloom could be considered an unpredictable resource and they are expected to be utilized by only a few specialized insects.

Height alone had no effect on species richness but when height and total leaf area were combined there was a small but significant correlation with the phytophagous fauna. However, height and total leaf area are correlated with each other, and the above relationship may result from the fact that, up to a certain point in the growing season, taller plants have more leaves.

No other studies have attempted to explore the role of the plant structure on the abundance of the whole insect community, including predators and parasites. Here it is shown that foliage complexity has a

will not detectable effect on the total arthropod fauna of goldenrods. This significance, however, may be only a residual effect of the highly significant linear relationship existing between the total leaf area and the phytophagous fauna. When natural enemies only are correlated with leaf area the relationship is negative and not significant. This fauna also shows a significant but negative relationship to height. It seems, however, that the observed negative relationships are only a matter of coincidence. Natural enemies may be abundant on a given plant for reasons that are not related to the plant morphology. Plant density and plant population size affects the herbivore population (Price et al., 1980). Increased host density implies higher resource availability to herbivores, resulting in larger populations which will attract more natural enemies to the plant. Associated plants which are a source of nectar and pollen to adults, predators, and parasites may attract larger numbers of natural enemies to the host plant (van Driess, 1986). The presence of honeydew producing herbivores is also attractive to natural enemies (Price et al., 1980). The larger exemplifying rates observed in the present study occurred at B. P. East and Rocky Ridge in which goldenrod plants were infested with aphids during most of the growing season. Natural enemies of aphids were constantly collected, as well as other predators and parasites. The second highest rate was observed at St. Ed. Ave. which was the largest patch and where plant density was up to four times higher than at the other locations. The third highest exemplifying rate was found at a location with high plant diversity (Gardner Road) where the goldenrod plants grew mixed with a variety of other flowering weeds. These observations confirm the results of former studies related to abundance of natural enemies. They suggest that the

surrounding vegetation, the structure of the insect community and host plant density determine the diversity of predators and parasites. The results also support the view of many biological control workers who favor strips of natural vegetation growing between and around crop fields to increase diversity and offer alternate food and shelter for natural enemies (Allison, 1959).

The within-species variation in plant structure and insect diversity explained Price and Allison's (1980) observations of the importance of environmental conditions in determining population size of herbivores. These authors surveyed six species of arthropods which occurred in order on a moisture gradient from wet to dry soil conditions. Plants of the same species growing in more moist conditions were richer in herbivore-species and abundance. The study was restricted to 13 insects specific to arthropods. It was suggested that the humid conditions directly affected survival and development of some of these species. Such a gradient of moisture was not observed among locations occupied by the same perennial species or among all locations. Effect of environmental conditions on performance of a particular insect was also not observed, since the whole fauna was being studied. More evident was the environmental effect on the plant, which in turn affected insect diversity. Populations of the same species under different physical and environmental pressures grew differently and in consequence supported different insect faunas. For example, *E. canadensis* growing on S. P. West was taller and had more total leaf area than at the other locations.

Certain insects may also affect the growth form of the plant. In 1984, the population of *E. canadensis* growing on Reddy Point was heavily attacked by *Trialeurodes vaporariorum* (Homoptera). Larvae of this insect

here into the growing tip, interrupting the terminal growth of the plant and inducing lateral growth of two or more branches. Each branch produced flower stalks and this significantly increased the overall architectural complexity of the plant.

Another factor influencing insect diversity of goldenrods in Gainesville was plant abundance. *S. fistulosus* growing at 38 18 Ave. supported more phytophagous and beneficial arthropods than at 401. Species richness was greater at the former location than predicted by its total leaf area, as shown by its deviation from the regression line in Fig. 3. Plant abundance was responsible for some of the variation in the number of overwintering species associated with British crows (Southwood et al., 1982). High densities influence the nutritional quality of the foliage, concentration of nectar and honeydew, microclimate (Price et al., 1978) and collection rates (Strong and Lewis, 1976). Abundance of *S. fistulosus* at 38 18 Ave. was 2.4 to 4.1 times greater than at the other locations. This population was also the largest among all, with more resources available to the insects. These facts probably had a significant influence on the number of insect species at this location.

Variation in the insect richness among the four goldenrod species is harder to explain. Differences between *S. lanceolatus* and the other host species might be related to its architectural complexity. The narrow leaves of this plant form a sparse canopy which probably allows much exposure to winds, insulation and other elements. Contrarily, *S. canadensis* and *S. fistulosus* have a more dense vegetation where the leaves can find food and shelter. *S. canadensis* was more common than the other goldenrod species in Gainesville. Insects are more likely to find and colonize hosts more frequently distributed. Research on

Mason (1981) showed that plant frequency explained some of the variation in the species richness of microlepidoptera on Finnish deciduous trees and shrubs. *E. canadensis* is commonly found on roadsides, fence rows and old fields in Delawareville, and this may be partially responsible for the larger number of insect species associated with this host.

The fact that *E. gigantea* supports a smaller number of insect species than *E. fruticosa*, although the latter has smaller total leaf area is probably due to the density effect discussed earlier. However, as opposed to the other host's insect and plant curves in Fig. 3, the insect curve of *E. gigantea* is under that of the plant, perhaps indicating that it's foliage is under-exploited. Backus Rd was the only population of *E. gigantea* found and it occurred outside Germantown city limits. At this location the plant grew associated with many other weeds. Host plants growing associated with other plant species may be less attractive to insects because its odors are masked by volatile chemicals produced by the other plants (Price et al., 1980). Thus, it seems that *E. gigantea*, growing at Backus Rd, is less apparent than the other *Eulalia* species because of its scarce distribution and association with many other plants, and this affected the diversity of its insect fauna. The possibility that most insects avoid *E. gigantea* or *E. laevigata* due to the low water content of their leaves or to the presence of allelochemicals, cannot be dismissed. It was shown in the previous section of this chapter that these two species had low water content which may have inhibited nitrogen assimilation efficiency by the beetle *Scaphisoma integrum* and the moth *Scaphomyia distincta*. Water is an important factor limiting herbivory (Bartholomew, 1976) and could very well

be influencing the number of insect species associated with 1. glaberrima and 2. truncatella.

The protective chemical or physical defenses of plants may also play an important role in insect species diversity. Part of the biomass on a plant may not be available to the insects due to the accumulation of allelochemicals (Pasey, 1984). Polyphagous phytophagous insects may be adapted to overcome such nutritional problems (Lawton, 1979). They could significantly enrich the fauna of plants with low chemical defenses. They would, however, avoid those plants displaying a history of defenses including qualitative and/or quantitative chemicals and low levels of substrates. Only the insects adapted to overcome these nutritional problems would inhabit those plants. In this case, a more vigorous foliage does not result in a richer insect fauna associated with the plant, since few insects would be able to exploit it. Research on the chemical composition of the four glaberrima species is necessary before the influence of protective chemicals and nutritional quality on the number of insect species associated with them can be understood.

In Salinasville, seedling appear in March. Each seedling produces a long, erect stem which originates from a seed or rhizome node. Leaves are added to the stem as the plant grows until late summer, when the resources begin to be allocated to reproductive structures. Several aerial stems arise from one clone, but in this study, each stem is considered an individual plant. No branches are produced. The growth of the vegetative parts of the plant is represented by elongation of the stem and addition of leaves, whose area becomes smaller as their number increases. New structures are added in the blooming season, when the plant starts to put out flower stalks. The availability of these new

structures, however, may not result in more architectural complexity of the plant, since it may coincide with senescence and dropping of many leaves. The overall complexity of a given species of *Heliothis* slightly increases (*H. fluitans* and *H. virescens*) or decreases (*H. zea* and *H. leucocollis*) in the fall.

In temperate regions, there is a seasonal progression of the insect fauna on a plant. The number of phytophagous insect species on a patch of bracken increases gradually, reaching a peak in late July and early August (Lambert, 1975). In a first analysis of these data, the author suggested that the variation in number of species of phytophagous insects was due to a declining quality of bracken as food during the growing season, because most of the summer the quality of proteins in the plasma is considerably below that usually regarded as optimal for many insects. At the same time, the levels of tannins, lignin, and silica increase. Lambert's findings were very similar to those of Paine (1956) on leaves of oak trees, and both authors agreed on the plant chemistry explanation for the seasonal variation in the phytophagous fauna of bracken and oak. In further discussion of these findings however, Lambert (1976) expressed the idea that plant architecture instead of plant chemistry might better explain the variation in the number of insects throughout the year. In the leaf blade apices, the bracken frond becomes architecturally more complex, so that in a mature frond it is possible for different species to exploit very different microclimatic and nutritional conditions such as the basal plasma or the frond tip. This idea is substantiated by the studies of Paine (1956) on oaks which show a parallel increase in habitat space (as a measure of plant development) and in insect diversity. Campbell (1977) found that the seasonal succession in species

of herbivores and saprophages reflected seasonal changes in the plant structure in two soft marsh communities.

The seasonal buildup of the phylogenetic fauna of the four species of goldenrod in *Sainsvillea* seems to reflect both the architectural and chemical composition of the plant. For all four species, the curves describing the seasonal progression of the insect fauna closely fit the hypothetical model proposed by Lawton (1978) for the interaction between plant architecture and chemical defenses during the growing season of a perennial herb. Goldenrod latex curves show a sharper drop in abundance than Lawton's model, perhaps indicating a greater effect of the decrease in food quality with the age of the plant. This effect is especially seen in *S. canadensis*, the plant species with a more complex foliage. In analysis of the changes in the chemical composition of the leaves of the four plant species throughout the year would effectively show the effect of the chemical and architectural components on the seasonal succession of herbivores. Model analysis of the curves in Fig. 8 suggest that, in the smaller species (*S. Tuckerm.* and *S. inermis*), plant architecture accounted for most of the variability in the latent population, while in the bigger and more complex plants (*S. gigantea* and *S. canadensis*) chemical composition played an important role. Perhaps large plants displaying an abundance of food and chemical utilize more chemical defenses against insect attack. Analysis of nitrogen and water content taken from leaves in the middle of the growing season (July) showed that *S. canadensis* has a lower nitrogen content. There is evidence that nitrogen content of leaves decreases with age (Peterson, 1980; Jensen et al., 1981). The nutritional quality of *S. canadensis* might become very poor late in the growing season and although there is

an abundance of foliage, it is not readily available to the insects. Values of *L. glauca* are not too far off from values reported in *L. fulvipes* and *L. lanceumifolia*. It's leaf water content is low but it is comparable to that of *L. lanceumifolia*. These observations support the idea discussed before that *L. glauca* may have protective chemicals which limit insect colonization.

In summary, the complexity of the foliage seems to be the main factor determining insect species richness associated with *Salix* spp. in boreal forest. However, environmental factors and plant density influenced variability within the same species and among species. Chemical composition and nutrient status may be the possible explanation for the residual variance observed when the above factors are excluded. The seasonal build-up of the phytophagous fauna seems to follow the chemical and architectural changes in the plant during the year.

CONCLUSIONS

Although native Turkey tends to have a more specialized fauna, the great majority of phytophagous insect species collected in goldenrod in Britain are polytopes. This is related to the fact that only one species of Hemiptera, the most represented group, is specific to goldenrod.

Among the insects which feed only on Solidago and Aster, seven species are considered to be potential biological control agents: one attacking roots, Arota arvensis (Tortricidae), two leaf miners, Agrotis intensa (Chrysomelidae) and Agrostis stictica (Tortricidae), two leaf miners, Agrostis sp. 1 and Chrysomelid sp. 2 (Chrysomelidae), and two attacking flowers and seeds, Chrysomelid sp. 3 (Chrysomelidae) and Agrostis sp. 2 (Tortricidae).

Only three insect pests of economic crops were found on goldenrod. All were Hymenoptera: the carnivorous plant bug, Agrostis linearis, the southern green stink bug, Agrostis viridis and the virus Agrostis sp. 4. These species, however, are highly polytopes, and say to feed associated with many other weeds. Thus goldenrods growing in or near agroecosystems should not be considered a threat to crop fishes for feeding these pests.

On the other hand, goldenrods are an 'incubator' for many others' species. Many adult predators and parasites are attracted to this plant for nectar and honeydew and 40 species of Hymenoptera were found associated with goldenrods.

The water and nitrogen content of the leaves of the four *Solidago* species studied had a significant effect on the performance of the beetle *B. latreysi* and the moth *B. distincta*. Both insects developed faster and had higher survivorship and fecundity on *B. fistulosa*, the host with high leaf water and nitrogen content. Although *B. caryocynella* had a significantly lower leaf nitrogen content, the insects' performance on this host did not differ from that on *B. gigantea* and *B. serotmifolia*. Low leaf water content of the last two species may have inhibited nitrogen assimilation efficiency and nitrogen accumulation rate by the larvae of the two insect species. The direct effect of low leaf water content was more evident on the performance of *B. latreysi*, which is an external feeder, than on *B. distincta* which is a leaf tier and thus behaviorally more protected against desiccation. Leaf nitrogen content is the principal factor affecting the development of the moth.

Total leaf area was the main factor determining insect species diversity of goldenrods. Plants with more foliage (number of leaves \times average leaf area) had more phytophagous and total insect species associated with them than plants with sparser foliage. The overall architecture of the plant was not correlated to species richness because the addition of flower stalks is not followed by a significant increase in the insect fauna. Height of the plant seems to have an indirect effect on insect species diversity indirectly, up to a certain point in the growing season, higher plants have more leaves. Height alone did not significantly affect the number of insect species associated with the plant. Environmental factors affected plant growth which in turn caused variation in species richness among populations of the same host species. Plant abundance also influenced insect diversity

beetles were numerous were available to herbivores. The richness of the beneficial fauna is not related to the plant structural complexity but to other factors such as the presence of isoprene-producing herbivores, host plant density and the presence of other shading plants.

Still, unexplained variations in the number of insect species associated with goldenrods were attributed to chemical defenses and nutritional quality of the host plant. Further studies are needed to test this hypothesis.

APPENDIX

Analysis of variance and correlation coefficients of the measures of the architectural complexity of the four boat plans, and criteria used to derive the architectural rating.

Table 31. Analysis of variance on height, total leaf area and size of flower stalks of goldenrods plants at three different locations.

Source of Variations	df	Height	Total leaf area	Size of Flower Stalks	
Mean Square					
1974					
					<u>df</u>
Location (L)	4	47666.72***	303245.32***	75357.50***	4
Month (M)	2	617083.72***	1040530.32***	273761.72***	2
L x M	17	2985.72***	1440471.22***	36337.72***	8
Error	1894	351.27	25837.12	10548.47	564
1985 + 1986					
					<u>df</u>
Location (L)	3	24458.40***	3424477.32***	94350.32***	3
Year (Y)	1	6252.12***	3040875.32***	383625.00***	1
L x Y	3	480.11***	717923.58***	38754.72*	3
Month (M)	2	491304.72***	450045.12***		
M x Y	2	2702.75***	991834.84***		
L x M	6	2583.72***			
L x M x Y	6	1113.72***	120676.82***		
Error	594	270.36	27153.72	10448.32	312

*, **, *** F value significant at the 05, 1% and 0.1% levels, respectively.

*df for size of flower stalks.

Table A3. Criteria used to derive an architectural rating for four species of *Salix*.

Criteria	Month	Score				
		1	2	3	4	5
Height	May	<50	45–65	65–75	75–90	>90
	July	<60	55–65	65–100	110–125	>125
	Sept.	<105	110–155	155–175	175–215	>215
	Oct.	<155	155–165	165–175	175–215	>215
Leaf Area	May	<100	200–300	300–400	400–500	>500
	July	<200	200–400	400–600	600–800	>800
	Sept.	<500	500–650	650–900	900–1100	>1100
	Oct.	<500	500–600	600–900	900–1100	>1100
Flower/ Stalk	Sept.	<125	125–140	140–155	155–170	>170
	Oct.	<150	150–170	170–200	200–250	>250

Table A3. Correlations of measures of the architectural complexity of building plants with the number of insect species associated with them.

	Height	Total Leaf Area	Overall Architect.	Partial Architect.
	----- Correlation Coefficients -----			
Phytostegus	-0.34	0.82***	0.13	0.82**
Acropictus	0.38*	0.63	-0.29	0.55
Total	-0.37	0.38*	0.00	0.33

*, **, *** Correlation coefficient significant at the 10, 5 and 0.5% levels, respectively.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School, and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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